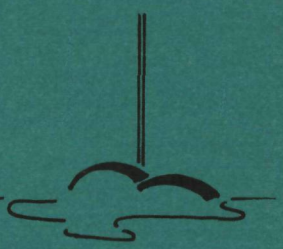
COMPONENT STUDIES IN SEAGRASS ECOSYSTEMS ALONG WEST EUROPEAN COASTS



RENÉ JACOBS

COMPONENT STUDIES IN SEAGRASS ECOSYSTEMS
ALONG WEST EUROPEAN COASTS

Promotor: Prof. Dr. C. den Hartog

COMPONENT STUDIES IN SEAGRASS ECOSYSTEMS ALONG WEST EUROPEAN COASTS

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN DE
WISKUNDE EN NATUURWETENSCHAPPEN
AAN DE KATHOLIEKE UNIVERSITEIT TE NIJMEGEN
OP GEZAG VAN DE RECTOR MAGNIFICUS
PROF DR J H G I GIESBERS
VOLGENS BESLUIT VAN HET COLLEGE VAN DEKANEN
IN HET OPENBAAR TE VERDEDIGEN
OP DONDERDAG 30 SEPTEMBER 1982
DES NAMIDDAGS TE 4 UUR

DOOR

RENÉ PETRUS WILHELMUS MARIA JACOBS
GEBOREN TE NIJMEGEN

1982
DRUK DRUKKERIJ VERWEIJ B V , MIJDRECHT

Aan mijn ouders en Maarten

This thesis includes a range of different aspects related to the ecology of seagrass. Such an approach would not have been possible without the cooperation of a number of graduate students, whom I would like to thank for their practical assistance, not to forget many most stimulating discussions. I have attempted to acknowledge the many people who have contributed in one way or another. Here I would like to thank any I have not mentioned.

The research work carried out from November 1975 to November 1979 was centered at the Laboratory of Aquatic Ecology (Catholic University, Nijmegen, The Netherlands) and I am most grateful to the head of the Department and all my former colleagues for their advice, helpful criticism and friendship.

CONTENTS

The foundations of the present-day knowledge of the anatomy and taxonomy of the eelgrass, Zostera marina L., were laid as far back as the mid-nineteenth century (e.g. Hofmeister, 1861; Duval-Jouve, 1873; De Lanessan, 1875; Clavaud, 1878; Areschoug, 1878; Schenck, 1886; Sauvageau, 1889, 1890, 1891; Ascherson and Graebner, 1907). The study of the plants in their natural habitat, and in relation to biotic and abiotic environmental factors, started at the beginning of the twentieth century (e.g. Ostenfeld, 1908; Joubin, 1909; C.G.J. Petersen, 1913, 1915, 1918; De Beauchamp, 1914; Setchell, 1929, 1933; Harmsen, 1936). Zostera marina, the most widespread seagrass species, is found along the coasts of the northern parts of the Atlantic and Pacific Oceans (Setchell, 1935; Den Hartog, 1970). The species came to be known under several common names (e.g. French, zostère; Dutch, zeegras; German, Seegras; Danish, baendeltang; etc.) and was found to be of both practical and nutritional value (see McRoy and Helfferich, 1980).

The suspected ecological importance of eelgrass (see Petersen and Boysen-Jensen, 1911) was confirmed by the locally catastrophic effects of the "wasting disease" in the nineteenthirties: entire beds in the North Atlantic coastal waters were destroyed and this resulted in fundamental changes in the substratum and the animal communities. The history, cause and environmental effects of the locally total disappearance of eelgrass have been described in numerous reports (e.g. Cotton, 1933; Cottam, 1933; Taylor, 1933; H.E. Petersen, 1933, 1934; Fischer-Piette, 1934; Marsille, 1935; Stevens, 1936; Renn, 1936; Tutin, 1938; Lami, 1938; Blegvad, 1944; Wilson, 1949). The slow and gradual recovery of the meadows was not complete until well into the fifties (Butcher, 1935; Cottam, 1945; Cottam and Munro, 1954). The history of the disease and the effects in Danish waters in relation to changes in the environment were reviewed by Rasmussen (1977).

Three years after the appearance of the first comprehensive monograph of the seagrasses of the world (Den Hartog, 1970), an International Seagrass Workshop was held in Leiden (The Netherlands),

which aimed at stronger cooperation in further seagrass research. In addition to a number of review papers (Den Hartog, 1973; McRoy and McMillan, 1973; Kikuchi and Pérès, 1973; Fenchel, 1973; Burrell, 1973), the Workshop group presented recommendations for further research on seagrass ecosystems (McRoy, 1973). The stimulating effect of the Workshop found concrete shape in a series of coordinated publications (McRoy and Helfferich, 1977; Phillips and McRoy, 1980; special issues of Aquatic Botany (Vol. 1(2), 1975; Vol. 2(2), 1976; Vol. 7(2), 1979) and Aquaculture (Vol. 4(2), 1974; Vol. 12(3), 1977)) in addition to a considerable list of reports on divergent topics related to seagrasses.

Since its foundation in 1973, the research projects at the Department of Aquatic Ecology of the Catholic University of Nijmegen (The Netherlands) have concentrated on the structure, function and dynamics of macrophyte-dominated aquatic communities (see Den Hartog, 1976b). Emphasis was laid on the communities dominated by nymphaeids (Lammens and Van der Velde, 1978; Van der Velde, 1979; Van der Velde et al., 1979; Van der Velde and Van der Heijden, 1981), Zannichellia spp. (Van Vierssen, 1982a, b, c; Van Vierssen and Van Wijk, 1982) and Ruppia spp. (Verhoeven, 1975, 1979, 1980a, b; Verhoeven and Van Vierssen, 1978a, b). The communities dominated by the seagrasses Zostera marina and Z. noltii Hornem. were investigated from 1975 to 1979 by the author in a research project aimed at the study of their structural and functional aspects, and was financed by the Netherlands Organization for the Advancement of Pure Research (ZWO). The study areas were located in the Netherlands, i.e. the Dutch Wadden Sea and the Oosterschelde in the SW, and in Brittany (France).

Seagrasses are the only angiosperms completely adapted to a permanently submerged life in the marine environment. A well-developed anchoring system is common to all seagrasses, differentiating them from other marine plants (Arber, 1920; Den Hartog, 1967, 1970). As a consequence they are able to compete successfully for space and substrate and to form extensive meadows, both in the eulittoral and sublittoral. Being the dominant plant species, the seagrass forms the

frame-work of the community and therefore formed a vital part of this study. The other major structural elements comprise the composition and the arrangement of the organisms in space and time, the mutual relations between the organisms and their relation to the surrounding environment (Den Hartog, 1976a, 1978, 1979, 1982). In general the community represents the structural component of the seagrass ecosystem.

Inherent to a study of an ecosystem is the difficult or impossible task of differentiating between structural and functional components of the system, as these are not completely independent of each other. The functional components comprise the characteristic relations between the community and the environment, expressed by production, decomposition, food chains, etc. Various aspects of the seagrass system were investigated more or less separately by the author, although the relations between the subjects were permanently reviewed. The research subjects were chosen in such a way that they bore a distinct relation to one or more of the other subjects. Though each is presented as an independent unit, the discussions in the reports aim to recognize those features which contribute to a better understanding of structure and function of the whole ecosystem. A number of these reports are included in this thesis.

A part of the Zostera project, which concerned the macrofauna composition of the eelgrass beds near Roscoff was started in May 1977. This programme was disturbed by the impact of the "Amoco Cadiz" oil spill in March 1978 (see Jacobs, 1979). However, the data collected before the spill enable evaluation of the impact of the discharge on the seagrass ecosystem. The preliminary results were given by Jacobs (1980) and Den Hartog and Jacobs (1980). More detailed information is presented in the last part of this thesis.

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Aquatic Botany, 7 (1979) 151—172

DISTRIBUTION AND ASPECTS OF THE PRODUCTION AND BIOMASS OF EELGRASS, *ZOSTERA MARINA* L., AT ROSCOFF, FRANCE

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(Accepted 23 March 1979)

ABSTRACT

Jacobs, R.P.W.M., 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. *Aquat. Bot.*, 7: 151—172.

A survey is given of the changes since 1909 in the area covered with eelgrass at Roscoff, France. In 1976, *Zostera marina* L. was distributed from mean low water mark at neap tide (MLWN) down to a depth of 4 m below mean low water mark at spring tide (MLWS). In these meadows, a relation existed between the aboveground biomass, length of leaves, number of shoots m^{-2} and the time of water coverage.

Biomass and production were studied from February 1976 to February 1977. The biomass of leaf blades, leaf sheaths, rhizomes and roots followed the same pattern with increasing total values from February (190 g dry wt. m^{-2}) to August (470 g dry wt. m^{-2}) and a decline in autumn and winter.

Production was measured by a leaf marking technique together with the determination of the plastochrone interval, i.e. the time interval between the initiation of two successive leaves; on the average, this value amounted to 19.3 days.

As the production of rhizome segments occurred at the same rate as that of the leaves, it was possible to estimate separately the production of leaf blades, leaf sheaths, rhizomes and roots during the year. The course of the production process, especially of the aboveground parts, seemed to be controlled by insolation. Annual net production was 1608 g dry wt. m^{-2}; 69% of this was aboveground production. Turnover rate of aboveground parts (1.5% per day) was higher than of underground parts (0.5% per day), corresponding with a turnover time of 68 and 193 days, respectively.

INTRODUCTION

The dominant marine angiosperm of the Atlantic coasts of Europe is the eelgrass, *Zostera marina* L. It usually occurs in large quantities and forms dense beds which cover immense areas in the coastal waters. At Roscoff (France) eelgrass is the frame component of the dominant bottom community; it is widely distributed, both under sublittoral and eulittoral conditions (den Hartog, 1970). Its distribution and biology have been earlier described by Pruvot (1897), Joubin (1909) and de Beauchamp (1914). After the wasting disease which destroyed most of the Atlantic eelgrass beds between 1930 and 1940, the recuperation took place mainly after 1960 (Blois et al., 1961).

It is known that a seagrass bed fulfils several functions: stabilizing the bottom, forming a substrate for epiphytes and epizoa and providing a nursery to many organisms (den Hartog, 1977). The most important function is, however, the large amount of carbon that is fixed by photosynthesis and becomes available via the detrital food chain.

Production of aquatic macrophytes can be determined in several ways, e.g. by measuring the changes in dissolved oxygen concentration in the water surrounding the plants or by incorporation of ^{14}C during photosynthesis. Since Hartman and Brown (1967) demonstrated that the oxygen produced by photosynthesis is stored and recycled in the internal lacunal system of the macrophytes, this method must be considered questionable. Moreover, the application of the ^{14}C technique in more recent studies (Dillon, 1971; McRoy, 1974; Brylinski, 1977; Penhale, 1977) is time-consuming and technically difficult. Because it is possible that CO_2 is recycled in the lacunae of the leaves (Wetzel and Hough, 1973; Hough, 1974), these experiments must be carried out during short incubations under defined conditions.

Methods of estimating production based on doubling the value of the maximum standing stock (Petersen, 1913; Mann, 1972) or on seasonal increases in biomass are not applicable to these communities because a correction for lost leaves is necessary (Westlake, 1965).

The method of leaf marking developed by Zieman (1968, 1974, 1975) has been used very successfully to measure leaf production in situ during a longer period of time. However, this method neglected the root and rhizome production. In this investigation, a modification of the leaf marking technique has been used together with a determination of the plastochrone interval, i.e. the time interval between the initiation of two successive leaves of one shoot (Tomlinson, 1972, 1974; Patriquin, 1973).

THE STUDY AREA

Roscoff is located on the north coast of Brittany at approximately 48° 44′ N and 3° 59′ W. To the east is situated the Bay of Morlaix with its muddy intertidal flats and to the west are sandy beaches with numerous rocky outcrops. The area between the island Ile de Batz, one kilometre to the north of Roscoff and the shore has a sheltered character (Fig. 1). The bottom consists here of sand and gravel.

Due to the great tidal range (up to 9.5 m), zonation is most distinct. The flora and fauna in this area consist of elements both from the northern (boreal) zone and the southern (lusitanian) zone. The water temperature changes very slowly and gradually (maximum values of 16°C in August and minimum values of 9°C in February) (see Fig. 8). The chlorinity is nearly constant: 19.4‰ (Anonymous, 1976).

The *Zostera marina* beds are the most extensive of the Brittany coast and they are situated in the area between the shore and Ile de Batz. The first detailed map with the distribution and extent of the beds was made by Joubin

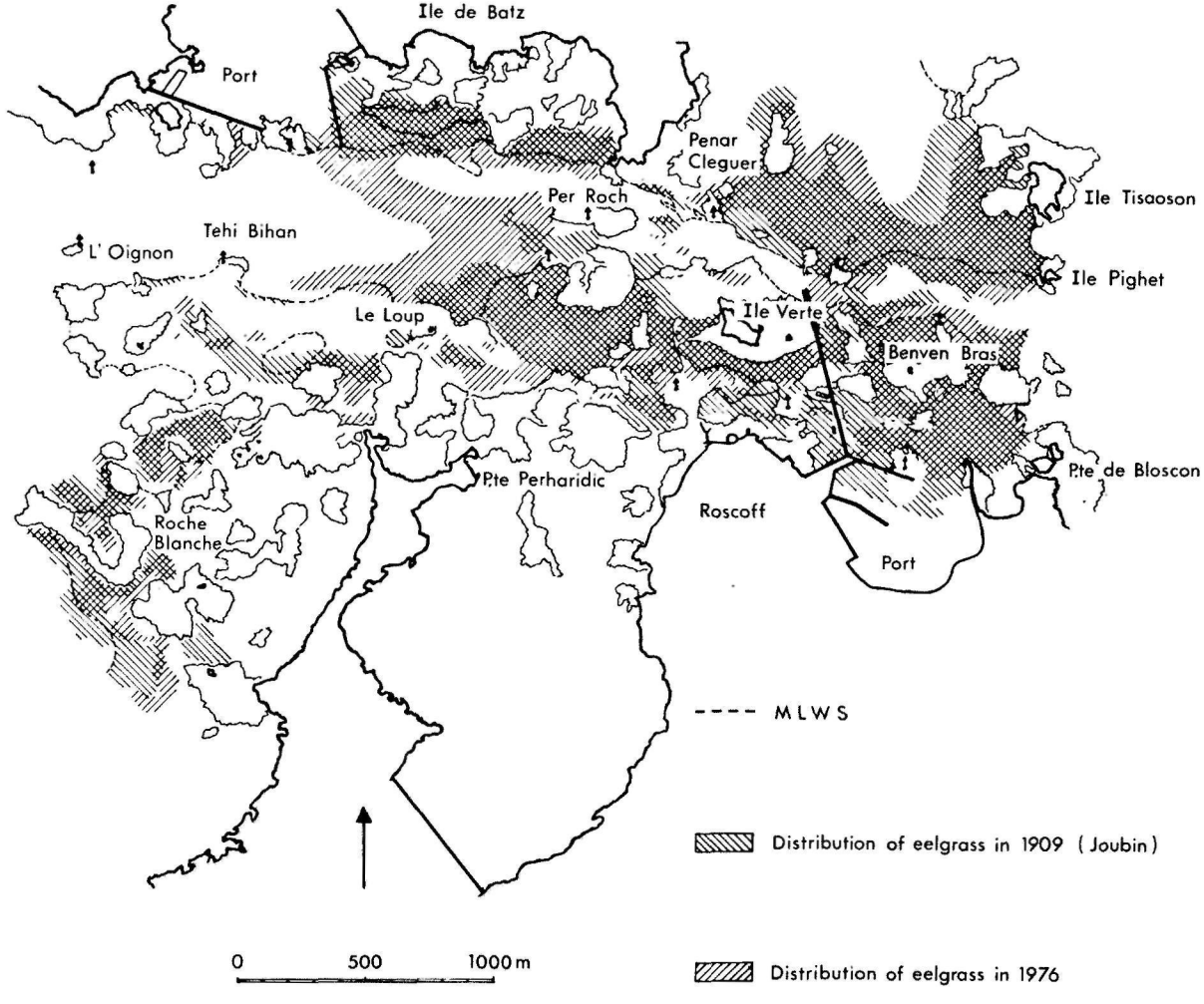

Fig. 1. Distribution of *Zostera marina* at Roscoff in 1909 (Joubin) and in August 1976.

(1909) (Fig. 1). From this map, the area covered by eelgrass was calculated as 11.6 km^2, of which 12.0% was situated below mean low water spring level (MLWS). Since 1909, the extent of the beds changed continuously, but the most profound changes took place during the 1930's. The history of the so-called wasting disease which caused the regression of eelgrass, was described by Lami (1933), Prenant (1934) and Renouf (1934). The effect of the almost complete disappearance of eelgrass on bottom sediments, flora and fauna has been reported by Prenant (1934), Tutin (1938), Dexter (1944) and Wilson (1949). The first recovery of the *Z. marina* populations in France was noted by Lami (1933) and Fischer-Piette (1934), but in 1957 the area covered by eelgrass was still less than that of 1909 (Blois et al., 1961). In particular, the sublittoral beds appeared almost completely absent (Fig. 2).

Since 1960, a strong recovery has taken place, but the extent of the meadows has changed constantly by erosion and recolonization (C. den Hartog, personal communication, 1975). These last changes have to be regarded as normal fluctuations of this seagrass community. In view of the succession, *Z. marina* is the initial colonizer as well as the dominant of the terminal stage of development of the community (Blois et al., 1961; den Hartog, 1973).

In 1976, the distribution of the eelgrass at Roscoff was mapped by means of aerial photographs. The area now covered by eelgrass (12.7 km^2) is more extensive than before the wasting disease; 21.6% of this is situated below

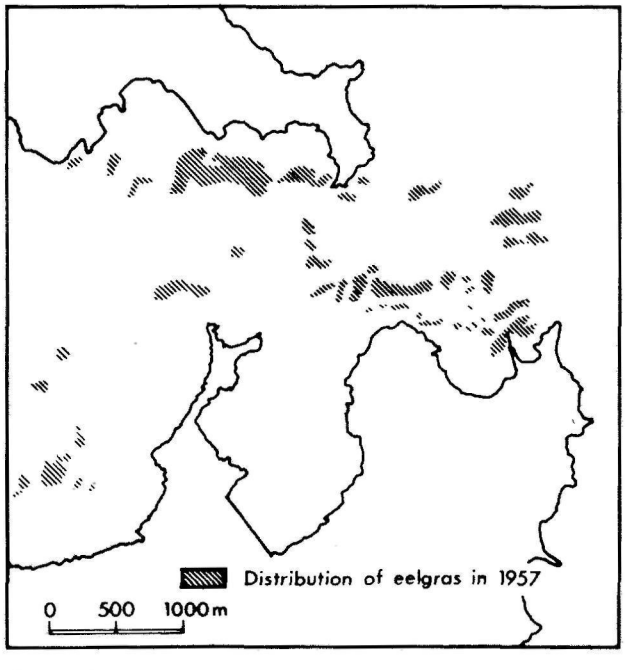

Fig. 2. Distribution of *Zostera marina* at Roscoff in 1957 (Blois et al., 1961).

MLWS level (Fig. 1). This means an important expansion of the sublittoral *Z. marina* vegetation. The upper limit of the area occupied by the species reaches the level of mean low water neap (MLWN). In the sublittoral, it descends to a depth of ca. 4 m (7 m below MLWN).

MATERIAL AND METHODS

Standing crop and tidal depth

In August 1976, the density of eelgrass shoots was determined at 17 sampling stations in the eulittoral. These stations met one of the following requirements: (a) a visual difference in the number of shoots m^{-2} and/or in leaf length; (b) a visual difference in the situation of the beds in the littoral. The absolute height of the selected stations was determined with a Wild levelling instrument.

At every station, the number of shoots was recorded in 50 × 50 cm quadrats. Within these 2500 cm^2, the length of the longest leaf blade of 50 randomly chosen shoots was measured, i.e. the length from leaf sheath to leaf tip. Only leaves with undamaged leaf tips were used. The eight sampling stations, which showed the greatest differences in leaf blade length and the number of shoots were selected for the determination of standing crop. At these sites, the plants within a quadrat of 20 × 20 cm were removed entirely (including roots) and taken to the laboratory. Here, the plant material was removed from the soil and separated into green parts and rhizomes by cutting the shoots in the meristematic region.

Epiphytic algae were removed from the eelgrass by careful scraping. As the remaining epiphytic biomass is mainly caused by the crustaceous, calcium carbonate-depositing red alga *Fosliella lejolisii* (Rosan.) Howe and diatoms belonging to the genus *Cocconeis*, the leaves were dipped in a bath of 8—10% phosphoric acid to remove the carbonates and to dissolve the extracellular mucous products of the diatoms.

The separate parts of the plants were then briefly rinsed in freshwater to remove sea salt, dried for 24 h at 90°C and weighed.

Productivity and biomass measurements

The study area was selected in an extensive, homogeneous eelgrass bed just to the south of Ile Verte (Fig. 1), in which way a good overall picture could be obtained of the production in the whole area.

A number of samples was chosen in such a way that the standard error of the mean was held at approximately 10%. A minimum number of four samples was necessary to fulfil this requirement.

A stainless steel frame divided into four equal parts of 20 × 20 cm was placed in the *Zostera* bed to mark the study area and was fixed with stainless steel pins in the corners. Of all shoots within the quadrats, the youngest leaves were marked individually with a staple. The number of shoots in each quadrat

was counted. After 2—4 weeks, the plants were removed and separated in the laboratory into above- and belowground parts. The number of marked shoots, new leaves produced on the marked shoots and new shoots were counted. The average plastochrone interval, i.e. the time interval between the initiation of two successive leaves on one shoot, was calculated as (D.G. Patriquin, personal communication, 1976):

$$P.I. = \frac{\text{number of shoots marked} \times \text{observation period (days)}}{\text{number of new leaves on marked shoots}}$$

By serial observations of marked shoots, the growth of individual leaves and their length at successive plastochrones could be determined (Fig. 3). It appeared that (1) the instantaneous growth rate of a leaf (after emergence above the leaf sheath) is the maximum growth rate, which decreases with the age of this leaf and (2) the length of the older of two leaf blades of one shoot is the length the younger would reach after growing for an interval equal to the difference in their age, i.e. the plastochrone interval. The same pattern in periodicity and leaf development has been found for *Thalassia testudinum* Banks ex König by Patriquin (1973). The growth of an individual leaf stopped after approximately 3 P.I.'s. Since each leaf corresponds to just one node, the production rate of leaves, rhizome segments and roots was equal.

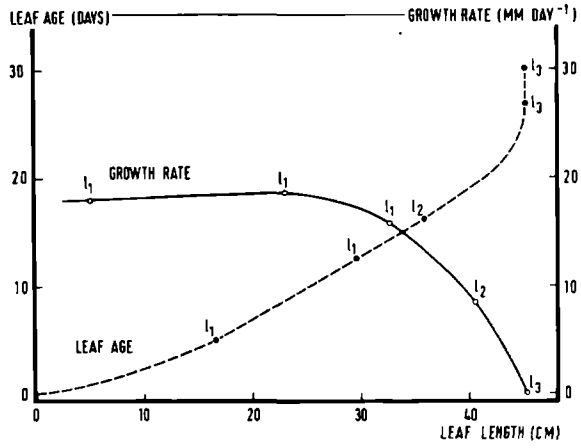

Fig. 3. Growth of an individual leaf blade of *Zostera marina*. The observed growth rates of one leaf blade on a shoot are plotted as leaf$_1$, l$_2$ and l$_3$ with a plastochrone interval of approximately 14 days.

The production of the different plant parts has been calculated as:

$$\text{Leaf blade production per shoot} = \frac{\text{average biomass of a fully formed leaf blade}}{\text{P.I.}} \quad (1)$$

$$\text{Leaf sheath production per shoot} = \frac{\text{average biomass of a leaf sheath}}{\text{average number of leaves per shoot}} \times \text{P.I.}^{-1} \quad (2)$$

$$\text{Rhizome production per shoot} = \frac{\text{average biomass of a fully formed internode}}{\text{P.I.}} \quad (3)$$

$$\text{Root production per shoot} = \frac{\text{average root biomass of a fully formed internode}}{\text{P.I.}} \quad (4)$$

The biomass of a fully developed "standard" leaf blade has been considered to be the average weight of a third leaf blade (average calculated from the biomass of all third leaf blades in the 4 quadrats). The biomass of a fully developed "standard" internode and its roots has been considered to be, respectively, the average weight of a fourth internode and its roots (average calculated from the biomass of all fourth internodes and their roots in the 4 quadrats). Although the third leaf blade of a shoot has the same length as the fourth leaf blade (Fig. 3), the biomass of the fourth leaf blade appeared to be greater than that of the third leaf blade, even after washing in phosphoric acid. Using the fourth leaf blade as the standard leaf blade would lead to an overestimation of the production. For this reason, the average biomass of the third leaf blade has been used for production calculations. Measuring the variation in length of the internodes of a shoot, only the fourth internode appeared fully formed. The fourth internode was therefore used as the standard internode for production calculations.

The removed aboveground plant material was separated into leaf sheaths and leaf blades; the latter were grouped according to their age with leaf 1 as the youngest leaf, and the leaf area index determined by measuring length and width. The belowground material was separated into dead and living rhizomes. Dead sections were black and fragmentary and living rhizomes were brown or white (mostly to a maximum of 10 internodes per shoot). All fourth rhizome segments (consisting of an internode and its adjacent node) and their two root bundles were collected. Dry weight determination of the separate plant parts was carried out as described above and subsamples were combusted for 3 h at 550°C to determine the ash content (Vollenweider, 1969).

During a plastochrone interval, just the length of a fully developed leaf blade is produced on a shoot, but most of this length concerns the two youngest leaf blades, as the leaf growth is restricted to these leaves (Fig. 3). New leaves on the marked shoots appear, on average, in the middle of the observation period. So the leaf length, produced during the observation period, can be regarded as a standard leaf blade approximately 1 P.I. after the middle of this period, i.e. 1.5—2.0 P.I.'s later than the beginning of the observation period. So, for calculation of the production, the values of P.I. were correlated with the values for the standard weights of leaf blade, leaf sheath, rhizome segment and roots 1.5—2.0 P.I.'s after the beginning of the observation period.

RESULTS

Standing crop in relation to tidal depth

Due to the presence of rocks and boulders in the study area, the eelgrass forms completely or partly separated rather than united beds. In the inner part of each bed, the eelgrass coverage is very uniform, being virtually 100%. The boundaries, however, change continually due to the influence of currents and wave action; they can be very abrupt after dislodging of the vegetation or very gradual in the case of colonization of the surrounding sandy bottom.

The number of shoots within the selected eelgrass beds varied greatly, from 390 to 2570 m^{-2}. The mean length of leaf blades (ranging from 16 to 61 cm) increased with decreasing number of shoots. Figure 4 shows the relation between the shoot density and the average leaf blade length. The calculated regression line is highly significant ($P < 0.001$) and obeys

$$\log y = -0.76 \log x + 3.77 \quad (r = -0.88)$$

The longest leaf blades were found in the beds in the lower littoral and sublittoral; with a leaf sheath length of approximately 25 cm, the maximum shoot length amounted here to 1 m.

The eelgrass standing crop per square metre was a function of the shoot density and leaf length: thus the average dry weight of aboveground plant parts within the established beds increased with leaf blade length and varied between 82 and 407 g dry wt. m^{-2}. A highly significant ($P < 0.001$) correlation exists between these two parameters

$$y = 5.04\,x + 30.14 \quad (r = 0.97)$$

of which the linear regression is shown in Fig. 5.

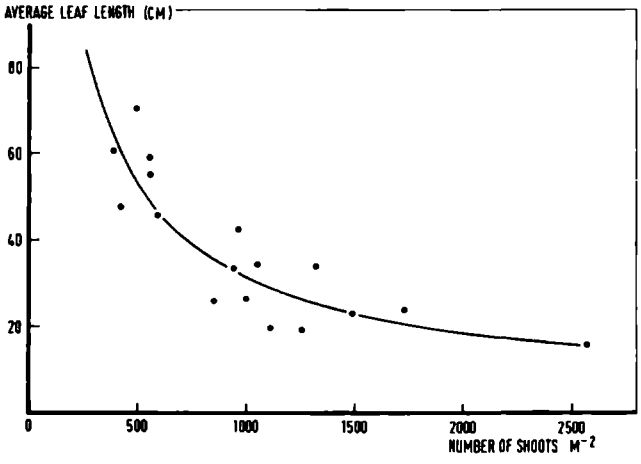

Fig. 4. The relation of shoot density to the average leaf blade length of *Zostera marina* stands at Roscoff.

TABLE I

Zostera marina at Roscoff. Standing crop and the average length of fully formed leaf blades in August 1976 in relation to tidal depth

Tidal depth (cm)	Standing crop (g dry wt. m^{-2})	Average leaf blade length (cm)
+ 340	81.8	15.7
+ 282	104.6	19.2
+ 330	173.9	19.6
+ 330	153.4	23.0
+ 300	220.0	34.3
+ 328	236.1	42.4
+ 270	294.8	59.0
+ 196	406.7	70.5

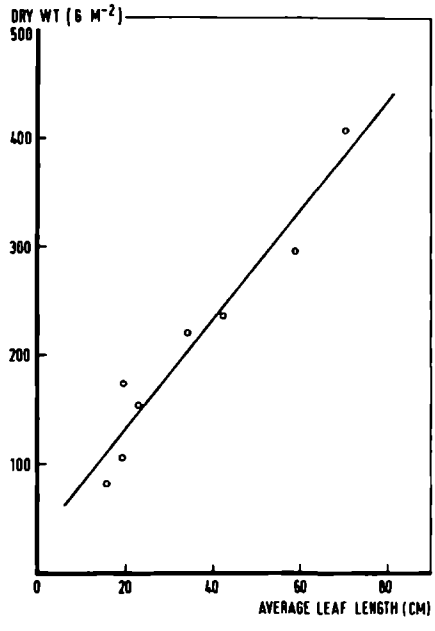

Fig. 5. Standing crop of *Zostera marina* stands as a function of the average leaf blade length.

The eelgrass standing crop generally increased with increase in tidal depth (Table I). Some of the beds, however, appeared to be situated at higher levels as could be expected from their relatively long leaf blades. This eelgrass grew in intertidal rock pools where water was retained at low tide by a threshold, or in beds with an elevated boundary which prevented the water flowing out. As sedimentation is greater in the marginal parts of the bed, the central parts are situated in a depression. At these positions, *Z. marina* is covered with water

for a time longer than the low tide period. It seems reasonable to conclude that the leaf blade length and the standing crop are more correlated with the percent water coverage, i.e. the percentage of time each contour is covered with water, than with the tidal depth.

Biomass, population dynamics and net production

The determination of biomass, population dynamics and net production was carried out from February 1976 to February 1977 in a *Zostera marina* community to the south of Ile Verte (Fig. 1). This bed is situated at approximately + 2.7 m in an extensive intertidal pool in which ca. 10 cm water is always retained at low tide.

Biomass

The biomass of leaf blades, leaf sheaths, rhizomes and roots followed a similar pattern in the course of the year, with increasing values from February to August and a decline in autumn and winter.

The biomass of the leaf blades was doubled from 61 g dry wt. m^{-2} in February—March to 131 g dry wt. m^{-2} in June—July. This increase was significant ($P < 0.02$). After the decrease in autumn, the leaf blade biomass reached the same level as at the beginning of the observation period.

The biomass of leaf sheaths showed a similar pattern with the minimum in February—March (31 g dry wt. m^{-2}) and a fourfold increase to 129 g dry wt. m^{-2} in July—August. The increase was significant ($P < 0.01$) and the same was true for the decline in autumn and winter ($P < 0.01$).

The rhizome biomass increased from 49 g dry wt. m^{-2} in March to 244 g dry wt. m^{-2} in September, a highly significant increase ($P < 0.001$). In February 1977, this rhizome biomass was halved (123 g dry wt. m^{-2}), but was still three times as great as in February 1976.

The root biomass increased from 50 g dry wt. m^{-2} in February 1976 to 70 g dry wt. m^{-2} in August, after which it decreased to 48 g dry wt. m^{-2} in February 1977. The root biomass was very variable due to adherent and practically unremovable mineral particles. Consequently, these results have not been used in further biomass comparisons.

The "biomass" of dead rhizomes varied from the minimum of 100 g dry wt. m^{-2} in March to the maximum of 253 g dry wt. m^{-2} in September. From October 1976, the "biomass" of dead rhizomes declined gradually to 122 g dry wt. m^{-2} in February 1977, indicating, in fact, a rapid decomposition.

The total biomass (minus roots) was 141 g dry wt. m^{-2} in March 1976; from April, this increased by ± 50 g dry wt. each month to a maximum in September (400 g dry wt. m^{-2}). The decline then occurred with a monthly average of 48 g dry wt. (Fig. 6). Aboveground parts formed 60—70% of the total biomass from February until August. Because of good protection against mechanical influences, the belowground parts formed the greatest part of the biomass in winter (up to 60%) (Fig. 6).

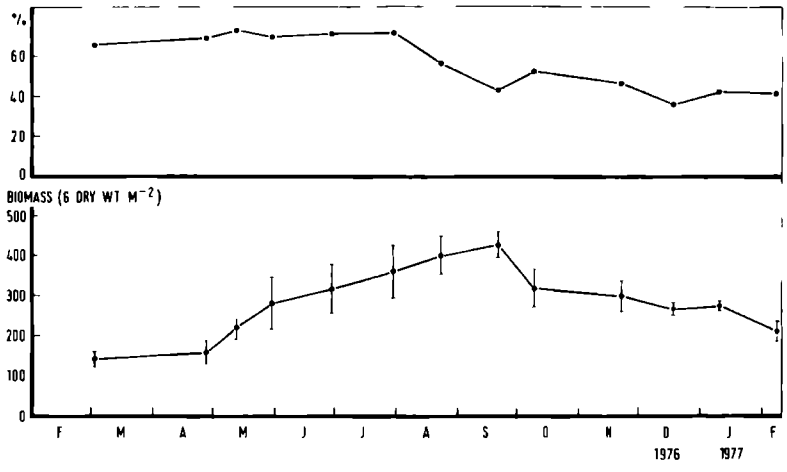

Fig. 6. Seasonal changes in *Zostera marina* biomass (minus roots) at Roscoff (mean ± standard error of 4 samples at each date is given) and the relative share of the leaves in the total biomass.

The ash content of leaf blades and leaf sheaths was almost constant, averaging 25% of the dry weight. This amount was much higher than was found by Sand-Jensen (1975), who determined the ash content to be 16.6%. The ash content of the rhizomes decreased from 26% of the dry weight in March to 16% in July—August and increased slowly after that to 25% in the winter. The ash content of dead rhizomes and roots was higher and more variable with a mean of 36% of the dry weight.

Shoot density

The number of shoots was greatest in May (about 700 m^{-2}). The increase in density from March 1976 to May 1976 coincided with the formation of lateral shoots by diffuse branching of the rhizomes (Tomlinson, 1974). During summer and autumn, the number of shoots varied slightly due to the apparent inhomogeneity of the vegetation and in the winter, a small decrease occurred which resulted in about 580 shoots m^{-2} in February 1977 (Fig. 7). Erect shoots with inflorescences have not been observed during the investigation period, at least not in the sample plots.

Leaves

The average number of leaves per shoot increased from February (3.8) to June (4.4) and showed a gradual decrease during summer and autumn to a minimum of 2.1 leaves per shoot in November (Table II). Because new leaves were produced continuously, the variation in the number of leaves per shoot was caused by a greater breakage of old leaves in summer and autumn than in spring.

Production of new shoots in spring initially caused a reduction in the average length of fully grown leaf blades from 40.0 to 23.8 cm, followed by a slow increase during summer to a maximum of 59.8 cm in December when the leaf blades of mature shoots contributed the greatest proportion to the community average (Table II). The variation in leaf blade length during the investigation period was great as storms and wave action influenced the length of fully grown leaf blades by breaking some off, especially the older, exterior ones.

Interestingly, the increase in spring of the number of shoots m^{-2} and the number of leaves per shoot coincided with an increase of the leaf area index (LAI), which resulted in more than a doubling of the index of the preceding

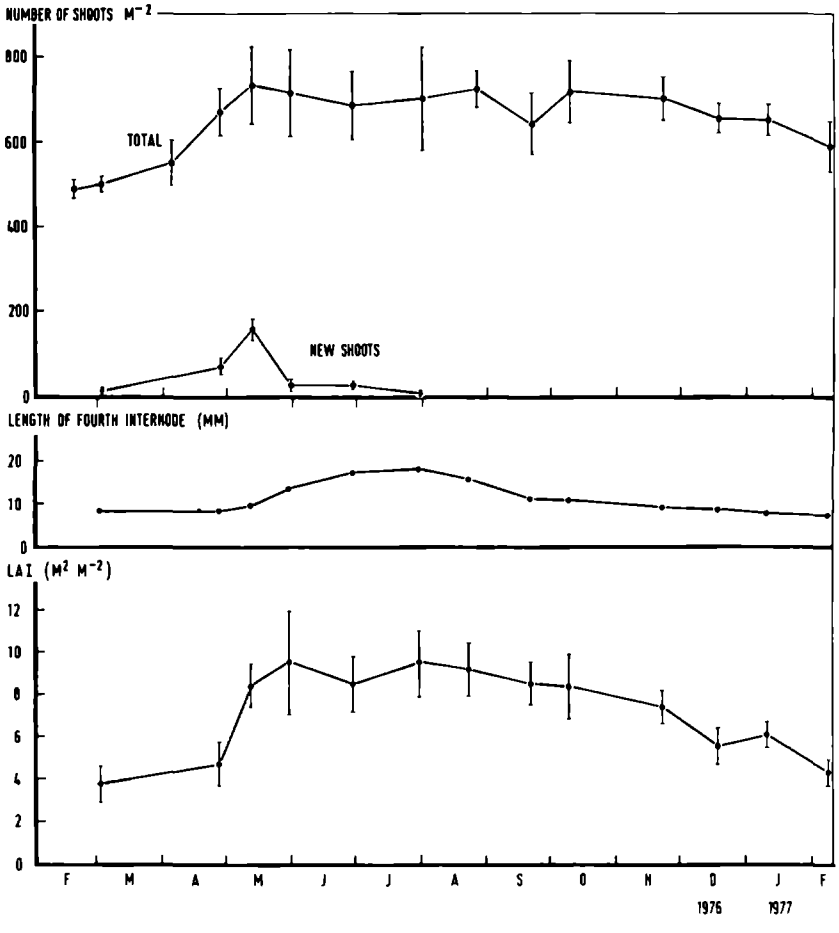

Fig. 7. Shoot density, average length of the fourth "standard" internode and leaf area index of *Zostera marina* at Roscoff. Mean ± standard error of 4 samples at each date is given.

TABLE II

Seasonal variation in the number of leaves per shoot and the length of fully formed leaf blades.
Means of a minimum of 80 shoots measured at each date are given.

Date	Number of leaves per shoot	Average leaf blade length (cm)
2 March 1976	3.8	40.0
27 April	4.1	23.8
12 May	4.0	35.5
30 May	4.2	32.8
29 June	4.4	32.7
31 July	3.4	47.9
23 August	3.8	44.0
21 September	3.3	41.3
9 October	3.1	49.8
22 November	2.1	46.2
18 December	2.9	59.8
10 January 1977	3.0	50.5
8 February	3.5	38.4

winter to 9.5 m^2 m^{-2} in August. The declining number of leaves per shoot in autumn and winter and the increasing leaf blade length at the same time was accompanied by a slow decrease of LAI in this half of the year (Fig. 7).

Rhizome

The average total length of living rhizomes varied from ± 35 m m^{-2} in winter to ± 75 m m^{-2} in August—September. Figure 7 shows the average length of the fourth "standard" internode with minima of 8.2 mm in March 1976 and 7.2 mm in February 1977 and a maximum of 17.8 mm in July. From the "standard" length in March, the number of shoots m^{-2} (± 500) and the total length of rhizomes, the number of living rhizome segments per shoot can be calculated as ± 10. The situation in July—August (± 700 shoots m^{-2}) resulted in a calculated total of 6 living rhizome segments per shoot. This reduction with regard to March is caused by the new lateral shoots with only a few rhizome segments.

Production

Marking of the leaf blades of *Z. marina* had no influence on the growth rate or production. Loss of the mark (a staple) by mechanical action during the observation period did not mean loss of the marked shoot, for two small holes remained in the youngest leaf.

In spite of the general pattern of leaf growth (Fig. 3) there existed a wide variation in individual plastochrone intervals. Consequently, the measured P.I.'s give only a reflection of the situation in the studied *Z. marina* bed.

The course of the P.I. showed a striking and reverse correlation with insolation (Fig. 8). The water temperature seemed of no importance: it rose gradually to a maximum of 16°C in August and declined after that to 9°C in February. However, these were values at high tide; at low tide, the air temperature (Fig. 8) played a more prominent part in the warming up of intertidal pools (to 25°C) and eelgrass beds without water coverage.

The increasing insolation in the first months of 1976 resulted in a faster formation of leaves and rhizome segments at a rate of one every 13 days in May. The sudden decline in insolation in June and July coincided with an increase in P.I. to 19 days in July, after which the level of the beginning of June was

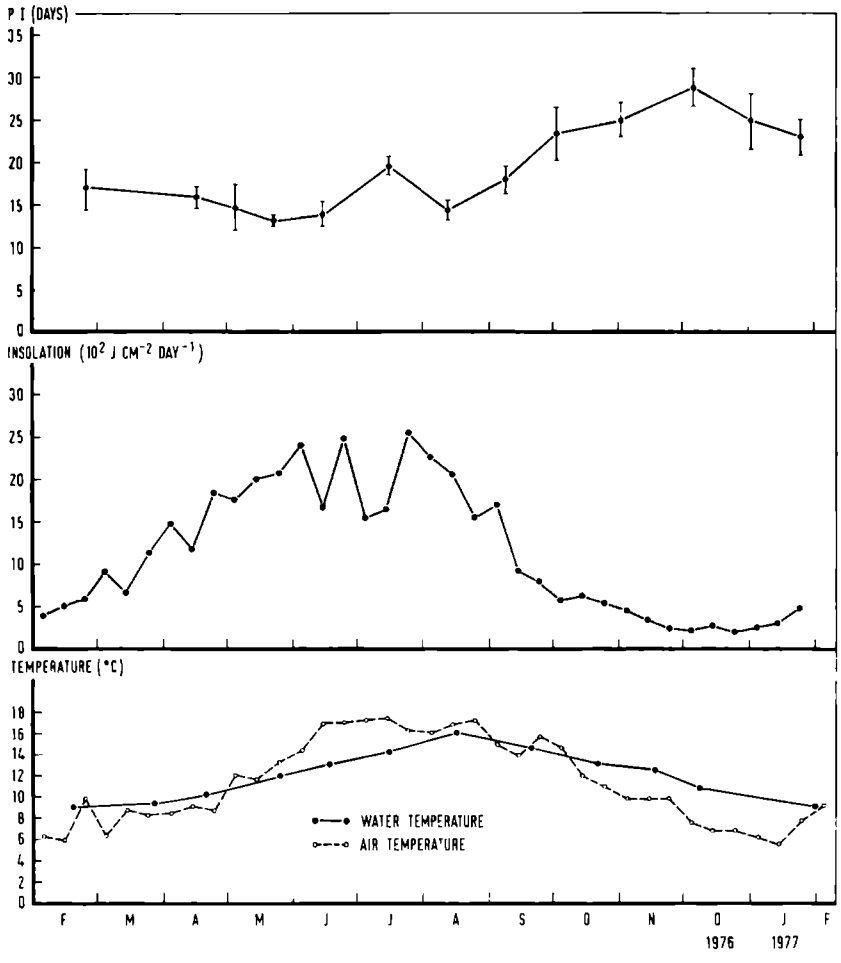

Fig. 8. Seasonal changes in plastochrone interval (P.I.) of *Zostera marina* at Roscoff (mean ± standard deviation of 4 samples are plotted in the middle of each marked period) compared with insolation and temperature. The air temperature and insolation are given as mean values for 10-day periods.

nearly reached again in August. The greatest P.I. in December (± 28 days) corresponded very well with the insolation pattern and so the decrease of the P.I., i.e. an increase in production rate of leaves, to the spring.

Based on the serial observations on P.I. and the variation in "standard" biomass of leaf blades, leaf sheaths, rhizome segments and their roots, the production has been calculated for every observation period (Fig. 9). The patterns of production of the different plant parts showed the same steady increase to May, a slight decline in the beginning of June followed by a strong recovery of only the aboveground production in July—August and from then onward an overall decrease to the end of the year.

Z. marina production clearly illustrated the effect of insolation, especially on the aboveground parts of the plant; graphs of insolation, leaf blade and leaf sheath production run parallel. However, the leaf blade production was, on average, 0.9 dry wt. m^{-2} day^{-1} higher than the leaf sheath production. Maximum production values of rhizomes (1.7 g dry wt. m^{-2} day^{-1}) and roots (2.8 g dry wt. m^{-2} day^{-1}) coincided in May with the appearance of new shoots, indicating an induction by increasing temperature and/or insolation. After May, the belowground production rapidly decreased and in September the minimum values were nearly reached.

The total plant production increased significantly ($P < 0.001$) from 2.7 g dry wt. m^{-2} day^{-1} in February 1976 to the maximum value of 8.7 g dry wt. m^{-2} day^{-1} in May. From June to the end of the year, it declined significantly ($P < 0.001$) to 1.7 g dry wt. m^{-2} day^{-1}.

Production of aboveground parts involved continuously the greatest share in the total, with the exception of the values for the month of May (Fig. 9), indicating the enormous expansion of the rhizome at that time. After May, the percentage showed an increase to the ultimate value of 86% in September, followed by a return to the initial level (± 75%) in winter.

By integrating the production curves, the net production for the whole year has been calculated as 1608 g dry wt. m^{-2}; 69% of this, viz. 1116 g dry wt., was aboveground production. Assuming an average ash-free dry weight of 25% of dry weight for the aboveground and 20% for the belowground parts of *Z. marina*, the organic carbon content can be calculated using the data of Westlake (1965), who showed that organic carbon contents of aquatic macrophytes varied between 43 and 48% of the ash-free dry weight, with an average of 46.5%. The so-calculated carbon percentage (Table III) of the aboveground parts (34.9%) falls within the range given by Harrison and Mann (1975), who found a percentage varying between 30 and 42% of the dry weight of leaves in the course of the year. To convert these results to kcal, the data of McRoy (1970) have been used. He found a caloric content of 4211 cal (g ash-free dry wt.)$^{-1}$ in leaves and 3571 cal (g ash-free dry wt.)$^{-1}$ in rhizomes. As shown in Table III, the net production of the whole year was 4932 kcal m^{-2}, i.e. 20.6 × 10^6 J m^{-2}. The total insolation during the same period amounted to 4137.8 × 10^6 J m^{-2}; thus, the production efficiency was 0.50%.

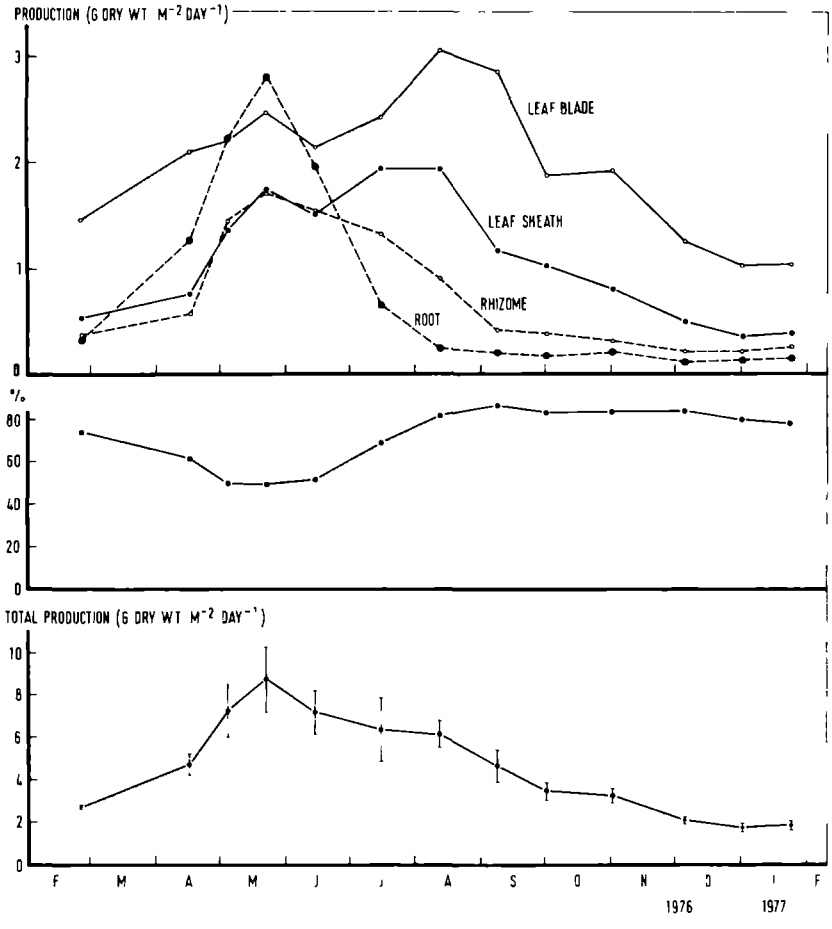

Fig. 9. Production of *Zostera marina* at Roscoff. Mean values of the production of leaf blades, leaf sheaths, rhizomes and roots, the relative share of the leaves in the total production, and total production (mean ± standard error of 4 samples are plotted in the middle of each marked period).

TABLE III

Annual production of *Zostera marina* at Roscoff

	g dry wt. m^{-2}	g ash-free dry wt. m^{-2}	g C m^{-2}	10^3 J m^{-2}
Aboveground parts	1116	837	389	14756
Belowground parts	492	394	183	5890
Total	1608	1231	572	20646

Turnover

Turnover rate is the fraction of an organism or population that is produced per unit time, mostly expressed as a percentage change per day. The average plastochrone interval concerning the whole observation period was 19.3 days, with a range of 13.1 days in May to 28.7 days in December (Fig. 8). The average number of leaves per shoot was 3.5 (Table II). So the average turnover rate of leaves was 1.5% per day with a maximum value in May (1.8%) and a minimum value in December (1.2%). The average turnover time, e.g. the average life time of leaves, was 68 days (ranging from 55 to 83 days). In total, 5.4 leaf crops were produced during the whole year.

In spite of the same production rate of leaves and rhizome segments, the values of turnover given above do not apply to the rhizome, as this consisted mostly of 10 living segments per shoot. So the average turnover rate of rhizomes has been calculated as 0.5% per day and the turnover time as 193 days, corresponding to 1.9 crops of rhizomes per year.

DISCUSSION AND CONCLUSIONS

Zostera marina has been recorded from various depths. In Denmark, Ostenfeld (1908) recorded eelgrass beds at a maximum depth of 11 m and Luther (1951) noted in South Finland a distribution from −1 to −6.8 m, with an optimum between −2 and −5.5 m. Decreasing irradiance would determine the lower limit of occurrence. Although, after the wasting disease in The Netherlands, only the eulittoral seagrass populations recovered (den Hartog and Polderman, 1975; Polderman and den Hartog, 1975), Nienhuis and de Bree (1977) showed that, after the closure of the Grevelingen estuary, the eelgrass extended down to a depth of about 7.5 m. Optimum depth with a maximum biomass appeared to be at −1 to −2 m. Nienhuis and de Bree (1977) concluded that, due to the reduction of irradiance, light would be a limiting factor in the vertical distribution.

At Roscoff, *Z. marina* grows to a depth of about 4 m below MLWS in a sandy bottom, which substrate is also available below this level. Because of a supply of ocean water with gradually changing temperature and a strong current along the coast, the water temperature at a depth of 30 m is hardly different from that at 0 m (Anonymous, 1976). As all abiotic key parameters except light are consistent throughout the depth, this is the most likely limiting factor responsible for the lower limit of eelgrass.

The upper limit of *Z. marina* at Roscoff is influenced by the time of water coverage (e.g. tidal pools) and the period of desiccation at low tide. Keller and Harris (1966) found eelgrass in Humboldt Bay (California) at places with a minimum tidal coverage of 85% and optimum growth from 95 to 100% tidal coverage. It seems likely that desiccation affects the vigour and vegetative reproduction of eelgrass in a similar way as it affects other aquatics (Strawn, 1961). The physiological effect of desiccation has hardly been studied in *Z.*

marina. Research with *Z. japonica* Aschers. and Graebn. (under the name of *Z. nana*) showed that weak dehydration had little influence on the photosynthetic rate, but strong dehydration was abruptly suppressive (Ogata and Matsui, 1965). However, at Roscoff, eelgrass also grows above the contours which are exposed to air for more than 15% of the time, namely in the intertidal pools and the beds with an elevated boundary, filled with stagnant water at low tide. In these pools, photosynthesis is not suppressed by dehydration, but can be suppressed by hypertony as a result of salinity change and temperature, as can be concluded from experiments by Ogata and Matsui (1965) with *Z. japonica* and by Biebl and McRoy (1971) with *Z. marina.*

Keller and Harris (1966) found an increasing biomass with tidal depth to a maximum between +0.3 and —0.5 m, which was quite similar to that reported by Backman and Barilotti (1976) for eelgrass beds in a coastal lagoon in southern California. In the sublittoral, they found a linear relationship between biomass in g dry weight and shoot density. With experiments in shaded and unshaded areas, Backman and Barilotti (1976) showed that shoot density was a function of the irradiance the plants receive; the same relationship existed with increasing depth. Giraud (1977) observed the same phenomenon in beds of *Posidonia oceanica* (L.) Delile in the Mediterranean: an increasing depth resulted in a decreasing number of shoots m^{-2}, provided the substrate was similar.

Backman and Barilotti (1976) presented no data about a possible variation in leaf length in relation to depth in the sublittoral, while Keller and Harris (1966) reported an increasing length with increasing tidal depth, i.e. the percent water coverage, as was also found in this investigation. It seems reasonable to conclude that, in the eulittoral, the maximum leaf length is determined by the percent water coverage: the leaves grow to a point just below the average water level, as was also shown by Koch et al. (1974) for *Thalassia testudinum* in culture experiments.

From the results of Keller and Harris (1966), Koch et al. (1974), Backman and Barilotti (1976), Giraud (1977) and the results of this investigation at Roscoff, an overall scheme can be drawn up of eelgrass growth in relation to tidal depth.

(a) Shoot density decreases with depth due to the irradiance the plants receive.

(b) Eelgrass standing crop increases with depth to a maximum between +0.5 m and —0.5 m, followed by a decrease.

(c) In the eulittoral, a linear relationship exists between standing crop and leaf length, apparently determined by the percent water coverage, and a hyperbolic relationship ($\log y = -a \log x + b$) between leaf length and shoot density, where y is the leaf length in cm and x is the number of shoots m^{-2}.

(d) In the upper sublittoral, a linear relationship exists between shoot density and standing crop (Backman and Barilotti, 1976). A restriction must be that at these depths the length of the leaves is more or less equal.

As also reported by several investigators (McRoy, 1969; Phillips, 1972; Har-

rison and Mann, 1975; Sand-Jensen, 1975) vegetative growth occurred during the winter months, even under Arctic ice (McRoy, 1969), at temperatures below 10°C, the temperature described by Setchell (1929) as the lower limit for growth of *Z. marina*. However, from Figs. 8 and 9, it is evident that vegetative growth continues below 10°C: it is primarily controlled by insolation and not by temperature, as has been shown also by Sand-Jensen (1975). At Roscoff, a low production rate and a low shoot density occurred in the same period that insolation was near the winter minimum, and the increase in production and shoot density coincided with an increase in insolation. Thus, it can be concluded that insolation controls the shoot density and the vegetative reproduction not only in relation with depth, but also during the year. This is also reported by Backman and Barilotti (1976).

Only a few investigators have studied eelgrass productivity in situ for a longer period of time. Grøntved (1958) used the increase in biomass during a 6 month summer period as representative of the net production. However, taking into account the apparently high turnover rate of leaves and the extensive export of produced material, this method must lead to an underestimation of net primary production. Petersen (1913) calculated the annual production of *Z. marina* stands in some Danish waters by doubling the maximum leaf biomass. Odum et al. (1973) used a modification of this method, namely the doubling of the maximum total biomass. Since the year's production at Roscoff was 1608 g dry wt. m^{-2}, the maximum leaf biomass 257 g dry wt. m^{-2}, and the maximum total biomass 470 g dry wt. m^{-2}, the ratio of net annual production to maximum leaf biomass was 6.3 and that to maximum total biomass 3.4. Sand-Jensen (1975) who investigated the production of a Danish eelgrass bed from April to October, found a ratio of net production to maximum total biomass of 2.5. So, the doubling of the maximum total biomass as a general approximation of production appears unsatisfactory. This was to be expected for the Roscoff seagrass beds in view of the average turnover time of leaves (68 days) and rhizomes (193 days).

Sand-Jensen (1975) found an average plastochrone interval of 14 days for *Z. marina* in Denmark from 9 April to 16 October. For the same period at Roscoff, this value appeared to be 15.6 days and the mean for the whole year was 19.3 days. Studies on the tropical seagrass *Thalassia testudinum* (Zieman, 1968, 1974, 1975; Patriquin, 1973) have indicated that the growth pattern resembles that of eelgrass with a P.I. of 14 days in the warmer months.

A comparison of the techniques for measuring the net primary production of *Z. marina* appears to be difficult, because the technique based on the determination of the plastochrone interval can be applied in situ during a longer time, while the inorganic ^{14}C uptake technique only agrees with production investigation during short incubation times under controlled conditions. Bittaker and Iverson (1976) showed with in situ experiments measuring production rates in *Thalassia testudinum* that the ^{14}C technique involved about 66% of the total leaf carbon production determined with the Zieman leaf marking technique. The difference (34%) resulted from the experimental design (sedi-

ment ^{14}C uptake, incubation chamber light energy absorption and differences in total light energy).

The measurement of the plastochrone interval appears to be a promising technique for the determination of production, not only of *Z. marina*, but also of other seagrasses. The applicability is more universal than the method of Zieman (1974), because of the possibility of determining the production of the different plant parts separately. Consequently, differences in the length of leaves, as also reported by Ostenfeld (1908), or rhizome segments, illustrating periodicity in development, can be compared with growth rate patterns, plastochrone interval and productivity.

ACKNOWLEDGEMENTS

I should especially like to thank my wife Regine, Frank Galle and Ries van der Camp, who provided practical assistance throughout this study. I am also indebted to Prof. Dr. C. den Hartog and Drs. G. van der Velde for critically reviewing the manuscript. The greatest part of the practical work was carried out at the Station Biologique at Roscoff and I thank the director, Prof. Dr. J. Bergerard, and his staff for their hospitality, and "Le Laboratoire de l'I.S.T. P.M. de Roscoff", which provided the temperature and insolation data. This investigation has been financed by the Netherlands Organization for the Advancement of Pure Research (ZWO).

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Aquatic Botany, 10 (1981) 45—60
Elsevier Scientific Publishing Company, Amsterdam — Printed in The Netherlands

PHENOLOGY OF REPRODUCTIVE SHOOTS OF EELGRASS, *ZOSTERA MARINA* L., AT ROSCOFF (FRANCE)

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ABSTRACT

Jacobs, R.P.W.M. and Pierson, E.S., 1981. Phenology of reproductive shoots of eelgrass, *Zostera marina* L., at Roscoff (France). *Aquat. Bot.*, 10: 45—60.

The development of flowering shoots and the maturation of flowers and fruits of *Zostera marina* L. were studied from May until the beginning of September 1978 at Roscoff (France) at two different tidal depths. Branches of flowering shoots matured acropetally, with the youngest branch as terminal inflorescence, and this also applied to the spathes within each branch. So, the development and maturation appeared to be a process starting at the base and proceeding to the apex of the shoot.

Within spathes, the number of flowers varied greatly. A close examination of the first order spathes showed that the number of flowers per spathe was positively correlated with increasing tidal depth and branch number and negatively correlated with the initiation time of the spathes. However, the ratio of one pistil to one anther was always found, although at the apex of the spadix some anthers sometimes failed to mature. A direct relation between the number of flowers per spathe and the mean length of the spadix and the spatial sheath could not significantly be demonstrated.

The mass flower production had already begun in the high-littoral bed in May, whereas this occurred in the lower bed one month later. However, the development and maturation of flowers and fruits occurred more quickly in the low-littoral bed than in the higher bed. As the ripening of fruits did not occur simultaneously, even within one spathe, this process could not be followed in situ.

INTRODUCTION

The eelgrass, *Zostera marina* L., is one of the most widely distributed and intensively studied seagrasses (den Hartog, 1970; McRoy and Helfferich, 1977). Nevertheless, there are only a few descriptions concerning the phenological patterns of the species and the factors influencing them, although notes on morphology and phenology are sufficiently available (e.g. Setchell, 1929; Tutin, 1938, 1942; Taylor, 1957; Keller and Harris, 1966; den Hartog, 1970; Phillips, 1972; Tomlinson, 1974; Jacobs, 1979). The results of these studies indicate that the application of a plant phenological index technique, as

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0304-3770/81/0000—0000/$02.50

proposed by West and Wein (1971) and Phillips (1976, 1980) in order to describe and quantify plant development, is very difficult in seagrasses. Temporal and/or spatial differences within one population, as a consequence of differences in tidal depth, temperature, light and soil characteristics make quantification most difficult. Moreover, phenotypic plasticity (e.g. annuals and perennials), as reported by Keddy and Patriquin (1978) and Gagnon et al. (1980), add to the difficulties in finding characteristics of the species population.

The basic description of the vegetative and reproductive growth of *Zostera marina* by Setchell (1929) has to be considered as the first one concerning the phenology of this seagrass. In his report, Setchell stated that the reproductive activities (anthesis and seed production) are confined to a rise in water temperature from 15 to 20°C. McRoy (1966, 1970) and Churchill and Riner (1978) found flowering stages in a period characterised by a rapid increase in water temperatures. These investigators agreed with Setchell (1929) that flowering occurs between 15 and 20°C. On the contrary, Phillips (1972) and Harrison and Mann (1975) showed that in Puget Sound (Washington) and Nova Scotia (Canada), respectively, sexual reproduction occurred at water temperatures below 15°C. However, quantitative data about the development of flowering shoots and maturation of flowers and fruits in situ are very scarce, because most investigators listed only the number of flowering shoots per m^2 (McRoy, 1970; Phillips, 1972; Felger and McRoy, 1975; Feldner, 1977). Only Philips (1972), Felger and McRoy (1975) and Churchill and Riner (1978) also determined seed production, and the last-mentioned authors also qualified the floral development.

It was the aim of the authors to study in situ, and to describe in detail, the whole process of the development of flowering shoots and the maturation of flowers and fruits of *Zostera marina* at two different tidal depths. Moreover, this investigation was started in order to describe the impact of the "Amoco Cadiz" oil spill on the eelgrass community. The tanker "Amoco Cadiz" went aground near Portsall on 16 March 1978, losing 220 000 t of oil. On 20 March, the first oil reached Roscoff, and during the following weeks there was direct contact between oil slick and eelgrass during each low water period. A primary survey of the impact on the eelgrass community at Roscoff and especially on its benthic fauna has been given by Jacobs (1980) and den Hartog and Jacobs (1980). This study was a part of an investigation of the possible effects on the eelgrass itself.

STUDY AREA AND METHODS

This investigation was carried out at Roscoff, which is located on the north coast of Brittany, France. Two homogeneous *Zostera* beds between Ile Verte and the shore (see Jacobs, 1979) were chosen as sampling areas, one just below mean low water neap mark (MLWN) and the other one ca. 1 m lower (maximum tidal range: 9.5 m).

In this area the water temperature changes very slowly and gradually (maximum values of 15°C in September and minimum values of 9°C in March) (see Fig. 1). However, at low tide on warm summer days the temperature may rise above 20°C in intertidal pools. The chlorinity is nearly constant with a mean of 18.4‰. For a detailed description of the study area and the extent of the eelgrass meadows, refer to Blois et al. (1961) and Jacobs (1979).

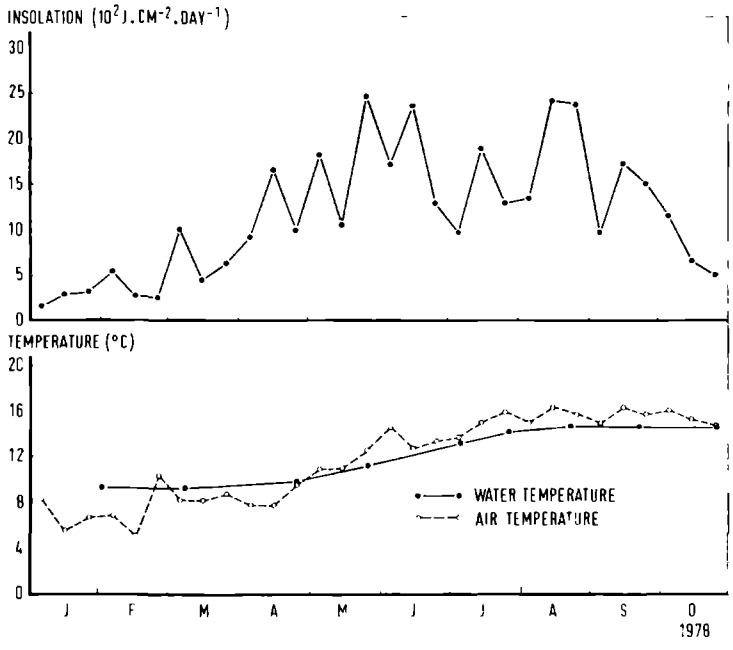

Fig. 1. Temperature and insolation characteristics at Roscoff in the period from January to November 1978. The air temperature and insolation are given as mean values per 10-day period.

Every month, from May to September 1978, 10—20 flowering shoots were collected in each bed by random harvesting (see Table I). These shoots were studied immediately to determine length and numbers of branches and of spathes, and the development stage of the spathes. On two dates in May (see Table II), the first and second spathe of each branch obtained from the high littoral shoots were examined for length and numbers of anthers and pistils. On two other dates (see Table II) the same was done with shoots from the low littoral eelgrass bed.

The data on temperature, insolation (Fig. 1) and chlorinity were obtained from the Laboratoire de I.S.T.P.M. de Roscoff, and concern the station 'NW Batz' (see Grall and Jacques, 1964), situated approximately 3.5 km from the study site.

TABLE I

Characteristics of the flowering shoots of *Zostera marina* at two different tidal depths at Roscoff from May till September 1978 (standard deviation is given in parentheses)

High littoral *Zostera marina* bed					
Date	3 May	30 May	30 June	29 July	21 August
No. flowering shoots examined	20	20	10	10	10
Mean total length (cm)	—	32 (12)	52 (27)	65 (15)	64 (8)
Mean no. branches shoot^{-1}	2.9 (0.7)	4.1 (0.6)	5.0 (0.6)	4.9 (0.7)	4.9 (0.3)
Mean no. spathes shoot^{-1}	3.0 (0.8)	7.3 (2.2)	13.2 (3.9)	20.3 (1.9)	18.8 (4.9)
Mean no. spathes branch^{-1}	1.0	1.8	2.6	4.1	3.8
Spathes closed in the prophyllum (%)	50	25	20	10	6
Visible spathes with closed sheath (%)	50	32	24	7	4
Visible spathes with opened sheath (%)	0	43	56	83	90
Low littoral *Zostera marina* bed					
Date	7 May	5 June	6 July	3 August	4 September
No. flowering shoots examined	20	15	10	10	10
Mean total length (cm)	77 (9)	60 (11)	67 (9)	62 (7)	57 (13)
Mean no. branches shoot^{-1}	4.0 (1.2)	4.9 (0.7)	4.7 (0.8)	5.0 (0.7)	5.0 (1.1)
Mean no. spathes shoot^{-1}	6.5 (3.7)	11.0 (2.0)	20.0 (3.0)	20.9 (3.5)	20.3 (4.5)
Mean no. spathes branch^{-1}	1.6	2.2	4.3	4.2	4.1
Spathes closed in the prophyllum (%)	38	48	20	16	8
Visible spathes with closed sheath (%)	52	40	20	3	0
Visible spathes with opened sheath (%)	10	12	60	81	92

TABLE II

Variations in length of spadix and spathal sheath of *Zostera marina* at Roscoff in 1978 (values represent data of the first-order spathes of different branches, with branch 1 as the basal one)

Situation *Zostera* bed	High in the littoral									Low in the littoral										
Date	3 May				30 May					7 May					5 June					
Branch number	1	2	3	4	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Mean length spadix (mm)	32.1	35.5	33.9	38.1	31.0	41.3	40.5	42.1	41.0	43.9	41.6	43.1	39.8	47.3	42.0	44.2	43.4	42.3	44.6
SD	4.3	4.0	5.8	4.3	8.3	4.2	5.6	4.0	5.5	7.1	5.1	6.6	6.5	5.8	7.7	5.4	6.6	5.8	5.8
n	9	10	9	8	7	6	6	7	7	10	12	14	13	10	15	14	15	13	11
Mean length spathal sheath (mm)	40.1	46.2	43.4	46.0	41.0	53.8	50.5	52.4	48.9	61.5	63.3	65.6	66.4	68.2	53.2	60.2	60.0	57.6	59.1
SD	5.7	5.3	4.2	4.2	11.7	6.2	8.4	5.7	7.8	4.9	8.2	8.4	6.2	6.7	9.4	8.5	7.9	4.0	6.2
n	9	10	9	8	7	6	6	7	7	10	12	14	13	10	15	14	15	13	11

RESULTS

Flowering shoot development

The generative shoots of *Zostera marina* are annual, terminal, erect axes, which are well differentiated from the horizontal axes by sympodial branching (den Hartog, 1970; Tomlinson, 1974). Each lateral branch of a flowering shoot is composed of a bundle of spathes (rhipidium). These branches are alternately arranged along the main axis (Fig. 2); one branch, usually only the first, can be composed of more rhipidia (Fig. 2). The branches matured acropetally with the youngest branch as terminal inflorescence.

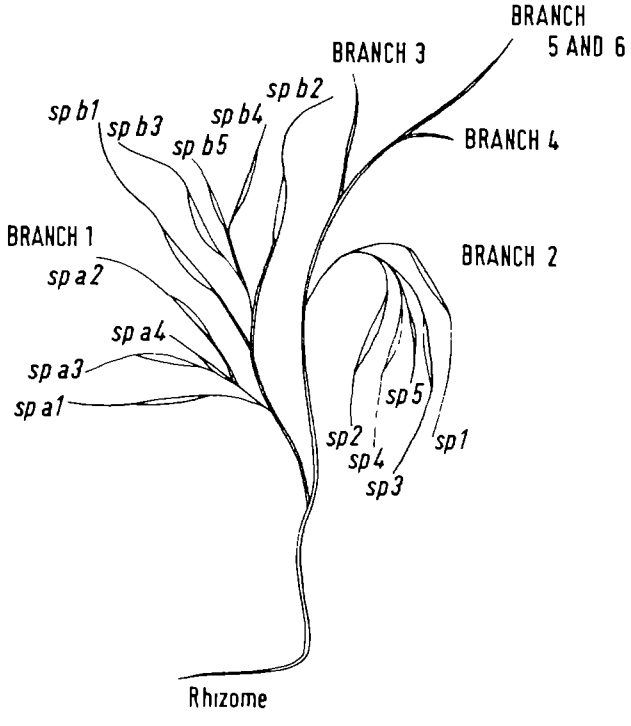

Fig. 2. Schematic representation of the flowering shoot of *Zostera marina*. Each branch consists of a bundle of spathes (rhipidium) with the youngest spathe (*sp*) as terminal inflorescence. One particular branch, usually the first one, can be composed of more rhipidia (here indicated as *sp a* and *sp b*).

The flowering shoots present in the study area were very irregularly dispersed. In the high littoral eelgrass bed the density varied from 0—70 shoots m^{-2} and comprised of up to 8% of the total number of shoots. In the low littoral bed the density was lower. The mean number of branches per shoot increased in the high littoral bed from 2.9 on 3 May to a maximum of 5.0 at the end of June and, furthermore, remained at this level, although the

mean total length of the flowering shoots continued to increase to 65 cm on 29 July (Table I). In the lower situated eelgrass bed, the mean number of branches per shoot at the beginning of May differed only slightly from the maximum (5.0), which was reached on 3 August. Surprisingly, the mean total length of the flowering shoots concerned decreased constantly during the period of investigation (from 77 to 57 cm) (Table I). The maximum number of branches per shoot was six, and in all samples from the low littoral eelgrass bed one or more shoots were observed with this maximum number of branches.

Each rhipidium is composed of a number of spathes, maturing acropetally along the axis as indicated by the numbers in Fig. 2. The mean number of spathes per shoot increased in the higher situated bed during the period of investigation to a maximum value of 20.3 on 29 July. At about the same time, the maximum for the lower bed was also found, which amounted to 20.9 spathes per shoot. A comparable course is shown by the mean number of spathes per branch, however with a somewhat earlier maximum for the lower bed (Table I). The following slight decrease to the end of August resulted from the breaking off of spathes with fruits or seeds. In addition, spathes heavily overgrown with epiphytic algae (mainly Ectocarpaceae and Bacillariophyceae) were easily broken off. The maximum numbers of spathes per shoot in the higher and lower situated eelgrass bed were 31 and 28, respectively.

Spathe development

When young, a spathe is enclosed by a tubular, membranous prophyllum. At a more mature stage of development, the spathe rises above the prophyllum and becomes distinctly visible. Along the peduncle the remnants of the prophyllum can sometimes be found (Fig. 3).

In the high littoral *Zostera* bed on 3 May, 50% of all spathes present were enclosed within their prophylla. In the lower bed this maximum was reached on 5 June (Table I). Comparing the data for the lower bed on 7 May with those from 5 June, it can be deduced that the production of spathes had already started, at a low level, in spring. However, the mass of development occurred in the beginning of June, approximately one month later than in the higher bed. During the period after the dates with the maximum values, the percentages of spathes closed within the prophylla decreased, but never became zero (see Table I). Hence, it can be concluded that at the end of the flowering season the production of new spathes continued.

Flower development

The spathe consists of a leaf blade and a sheath; the latter encloses a monoecious, lanceolate spadix, on which the male flowers (anthers) and the female flowers (pistils) are alternately arranged (Fig. 3). The smallest functional flowering unit consists of one pistil (ovary, style and two stigmata) and one anther (consisting of two free thecae connected by a ridge-like connective) (Fig. 3).

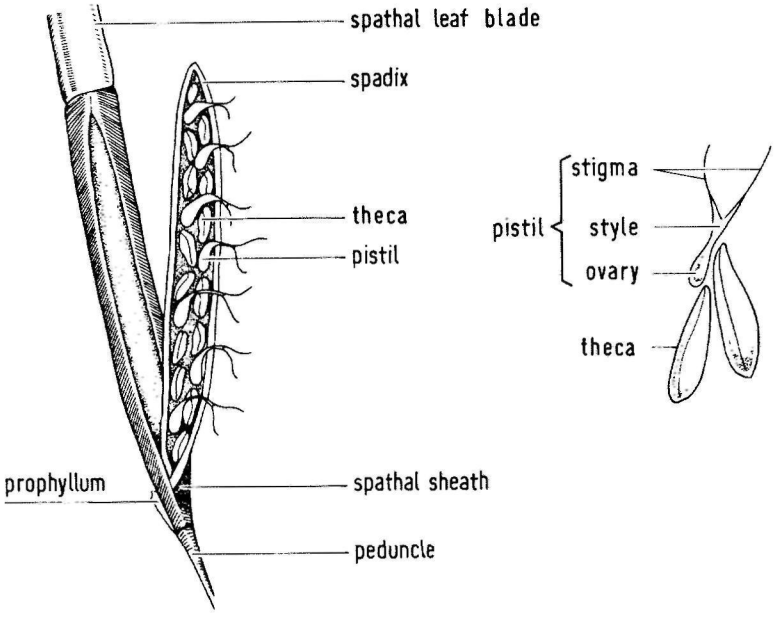

Fig. 3. *Zostera marina* spathe with an opened spathal sheath, showing the schematic arrangement of anthers and projecting pistils on the loosed spadix. To the right a flowering unit, consisting of one pistil and two thecae.

In this investigation the ratio of pistils to anthers of 1/1 has always been found. However, mature spathes often showed a lower number of ripe anthers than could be expected with regard to the number of pistils: some anthers near the apex of the spadix failed to develop further and to mature.

Within spathes the number of thecae and pistils varied greatly. However, some regularities appeared to exist: considering the mean number of thecae from spathes of the first order at comparable times, it is conspicuous that this value was distinctly lower on the same branch number in the high littoral bed than in the lower bed (see Fig. 4). In all cases, the mean number of thecae increased significantly ($P < 0.05$) for a specific spathe number from the basal branch to the terminal inflorescence. In all cases, the mean number of thecae from the second-order spathes was lower (9.7% on average) than the number from the first-order spathes on the same branch. This decreasing number of flowers per spathe within a rhipidium with increasing order number was also found by de Cock (1981) for annual eelgrass populations in The Netherlands.

Strikingly, both in the high- and the low-littoral bed at Roscoff the number of thecae per spathe from corresponding branch numbers decreased within one month (Fig. 4). The presence of flowers in the first-order spathes on all dates as shown in Fig. 4 supports the supposition that the development of the spathes of the last dates (30 May and 5 June) had started later; consequently also these flowering shoots were produced later than those investigated at the first two dates (3 May and 7 May). From this it may be concluded that

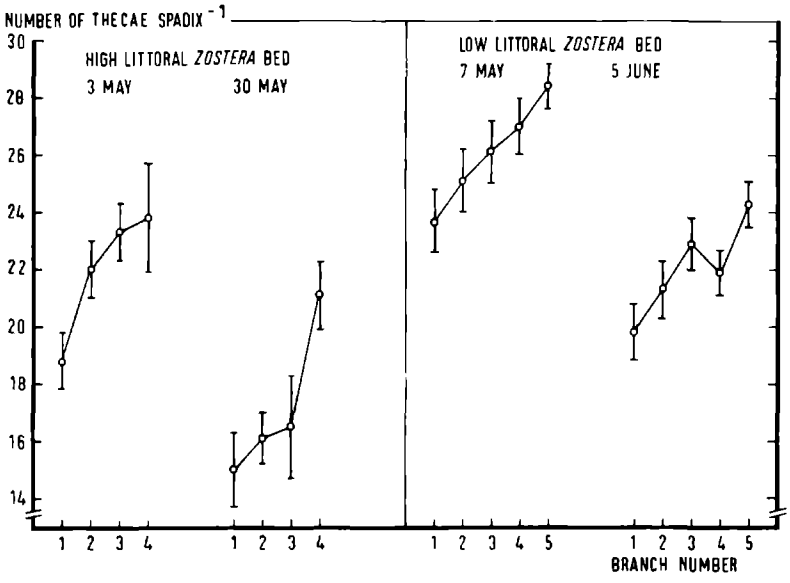

Fig. 4. Temporal and spatial variations in mean numbers (+SE) of thecae per spadix of *Zostera marina* at Roscoff. The values represent the numbers of the first-order spathes of different branches, with branch 1 as the basal one.

the numbers of anthers and pistils per spathe are dependent on depth in the littoral, initiation time of the spathes and of the branch number. The maximum number of anthers found on a single spadix was 16, so, the maximum number of flowers per spadix was 32.

Surprisingly, patterns in flower numbers as described above were only very vaguely recognizable in mean length of spadix and spathal sheath (Table II); these lengths were nearly independent of the total number of flowers per spathe. The mean spadix length varied between 31.0 and 47.3 mm, with a maximum value of 60.0 mm and the mean length of the spathal sheath varied between 40.1 and 68.2 mm, with a maximum of 83.0 mm, whereas the ratio spadix length to spathal sheath length ranged from 0.60 to 0.84 with a mean value of 0.75. All measurements are within the limits mentioned by den Hartog (1970).

Simultaneous development and maturation of the pistils of a single spathe resulted in a row of styles with two stigmata, projecting between the two flaps of the spathal sheath. The maturation of the anthers occurred later (proterogyny): thecae dehiscence followed on the abscission of the stigmata. Because of the fact that the exact period of flowering of female flowers was difficult to determine, this period was assumed to continue until the dehiscence of the thecae. Development and ripening of fruits on a single spadix did not necessarily occur simultaneously: at the same time, ovaries with widths of 0.8—1.6 mm were found. It was not, therefore, possible to make a distinction between spathes with young fruits and spathes with mature fruits.

In the high-littoral eelgrass bed, the most important development took place in May (up to 43% of all spathes had mature flowers), concurring with increases in shoot length, number of branches per shoot and number of spathes per shoot (Table I). Figure 5 shows that the cumulative curves of spathes with projecting pistils, spathes without anthers and spathes with fruits run nearly parallel, from which can be deduced that the development time between these stages took 15—20 days. The first ripe seeds were observed at the end of July. In August, the maturation of the anthers stopped and any further development of the fruits could hardly be determined, because the majority of the spathes (49% of the total number) became damaged and then detached by currents. This also happened quickly with spathes heavily overgrown with epiphytes. In a number of spathes, young specimens of the polychaete *Platynereis dumerilii* Aud. and M.Edw. were found (Jacobs and Pierson, 1979).

In the low-littoral eelgrass bed, spathes with projecting pistils and spathes without anthers were observed already in the beginning of May. However, during the month of May the production of spathes hardly changed. After May, the development occurred faster than in the higher bed with development times between the stages distinguished of 6--10 days. However, the development of the fruits seemed to be retarded from 6 July onwards (see Fig. 5).

On 7 May, the youngest spathes of all branches from seven flowering shoots

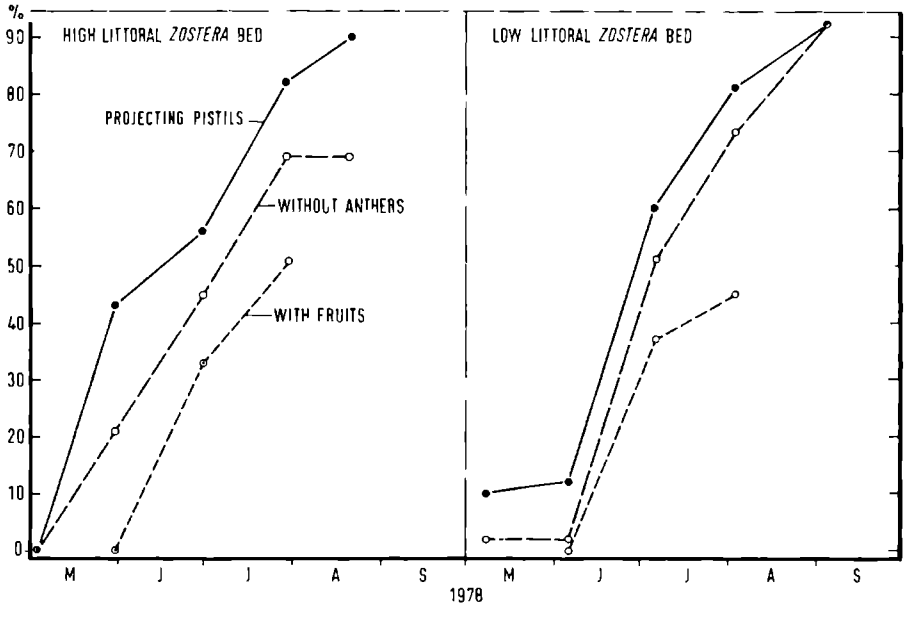

Fig. 5. Temporal development of *Zostera marina* spathes at two different tidal depths at Roscoff. The values represent percentages of mature spathes, according to which the successive stages distinguished are given cumulatively.

in the lower bed were marked with a staple in order to come to a determination of the plastochrone interval (P.I.), analogous to production measurements on vegetative shoots (see Jacobs, 1979). On 26 May (19 days later), there appeared to be nine new spathes on average on each marked shoot: a mean production rate of one spathe per shoot every 2.1 days. In the period from 5 June to 6 July, the number of spathes per shoot increased to 9.0 (see Table I), a mean production of one spathe per shoot per 3.3 days.

The potential seed production per shoot has been calculated as on the average 230 for shoots in the high-littoral bed and 273 for shoots in the low-littoral bed. In a single case, the number of seeds was determined (on 3 August). This provided 108 seeds from 10 shoots: on the average 10.8 seeds per shoot. However, this value was too low, because fertile ovaries and released seeds were not included, as in the case of abscissed spathes. On 4 September, 70% of all spathes were damaged.

DISCUSSION

Many investigators have noted the times of the initiation of flowering of *Zostera marina*. However, they used different criteria to describe the first flowering, e.g. the first flowering shoot, the first spathe or the first flowers. So, a comparison is most difficult. Moreover, all observations are only incidental records and are from scattered locations: from Roscoff (Obaton, 1954; Feldmann, 1954; Blois et al., 1961), from Denmark (Ostenfeld, 1908; Sand-Jensen, 1975), from the western Baltic (Feldner, 1977; J. Feldner, personal communication, 1979), from southern England (Tutin, 1938), from southern California (Backman and Barilotti, 1976) and from Nova Scotia, Canada (Keddy and Patriquin, 1978). The relationship between the moment of flowering and temperature has been discussed by Setchell (1929). Based on the observations of Duval-Jouve (1873), from the Mediterranean coast, Setchell called attention to the phenomenon of a flowering period later in the season as one proceeds northward. This suggested relationship with latitude is confirmed by data from some European floras (see Table III). Setchell (l.c.) stated that only the temperature controls growth of *Z. marina*, by which reproductive activities are restricted to 15—20°C. This agrees with data of McRoy (1970), Felger and McRoy (1975) and Churchill and Riner (1978), who described anthesis and seed production at temperatures at or above 15°C. Nevertheless, Phillips (1969, 1972) and Harrison and Mann (1975) showed flowering under conditions of 8—9°C, whereas this occurred at Roscoff at temperatures of 10—15°C under high water conditions (see Fig. 1) and sometimes higher temperatures during low water periods on sunny days. These latter data show the need for examination of other environmental factors, e.g. irradiance, for which the same relation with latitude applies as for temperature.

The importance of irradiance is also suggested by the following data. In Alaska (McRoy, 1970), in Puget Sound (Phillips, 1972) and also at Roscoff (during this investigation), eelgrass situated higher in the littoral produced

TABLE III

Comparison of the beginning of the flowering season of *Zostera marina* according to some European floras (countries arranged approximately in order of increasing geographic latitude)

Country	Beginning of flowering period	Reference
Portugal	June	Coutinho (1939)
France	June	Coste (1937)
Belgium	June	Mullenders (1967)
The Netherlands	June	Heukels and van Ooststroom (1973)
Ireland	July	Webb (1967)
England	July	Butcher (1961)
Denmark	July	Jørgensen (1973)
Sweden	July	Weimarck (1963)
Iceland	August	Stefánsson (1948)

more flowering shoots than in the lower beds. McRoy (1970) implied this difference to higher temperatures in tidepools in comparison with subtidal conditions. However, taking into account that for the irradiance the same relation exists with increasing depth, and the fact that Backman and Barilotti (1976) showed in experiments under shaded and unshaded conditions that flowering is affected by reduced irradiance, it might be concluded that the first stage in the flowering process, the induction (initiation) of flowering shoots, is primarily correlated with the irradiance the plants receive. This suggests a direct relation between the appearance of new shoots and changes, particularly increases, in isolation. The same relation has been found for the vegetative growth of *Zostera marina* (Jacobs, 1979). This suggestion is supported by the fact that during August—September 1978 at Roscoff, the increasing insolation (see Fig. 1) coincided with the appearance of new vegetative shoots in the eelgrass beds.

Several factors influenced the length of flowering shoots. The length was positively correlated with an increasing depth. This was confirmed by some observations at the level of LLWS, where flowering shoots have been found with mean lengths of 120 cm. Moreover, growth characteristics, e.g. an increasing number of branches per shoot, were responsible for an increasing length during the season (see Table I). Assuming the same influences on the length in other populations, only a rough comparison, based on maximum values, is possible with data from literature.

Setchell (1929) noted along the Pacific coast of North America lengths up to 3 m and according to Felger and McRoy (1975) eelgrass flowering shoots in the Gulf of California may attain lengths of 1—3 m at depths of 8—10 m. Along the Atlantic coast of North America, Setchell (1929) collected flowering shoots with lengths up to 1.2 m and Churchill and Riner (1978) noted lengths of 19—48 cm (32 cm on average) at 1 m below MLW. Keddy and Patriquin

(1978) found flowering shoots on intertidal mudflats and in creeks with increasing length during the season to a maximum of 70 cm. These size variations probably reflect differences in depth distribution rather than differences between Pacific and Atlantic varieties as suggested by Setchell (1929). This is confirmed by findings of *Zostera marina* in Danish waters (Ostenfeld, 1908), where lengths of flowering shoots increased to a maximum of 2.5 m at a depth of 8 m. These data suggest a relation between the length of fully grown flowering shoots and water depth. Therefore it seems reasonable to conclude that, analogous to vegetative shoots (Keller and Harris, 1966; Jacobs, 1979), the length of flowering shoots in the intertidal area is positively correlated with the percentage water coverage, i.e. the time interval each contour is covered with water, and in the sublittoral with depth.

Besides spatial differences in shoot length and number of flowers per spathe between the lower and the higher eelgrass bed, there also appeared to be some temporal differences. The increase in the mean number of branches per shoot over time was a consequence of the following: (1) a non-simultaneous, i.e. an acropetal, development of the branches on a single shoot, a phenomenon which is at variance with the observations of de Cock (1981) who found in an annual eelgrass population in The Netherlands that after the production of all branches, all first-order spathes flowered at the same time, followed by the flowering of the second-order spathes; and (2) a non-simultaneous production of flowering shoots, resulting in deviating numbers of branches on shoots produced later in the season. The production of new flowering shoots can also explain the decrease in shoot length during the investigation period. Corresponding with this phenomenon is the decreasing length of spadix and spathal sheath of the later-produced spathes. One may speculate that the temporal differences described above were a consequence of the high production values of flowering shoots (e.g. each 2--3 days one spathe per shoot), caused by increasing irradiance and/or temperature, and suggest a nutrient stress. Such a phenomenon would be analogous to the decreasing lengths of vegetative shoots in a comparable period in 1976 with high production rates (Jacobs, 1979).

The results of this study show the difficulty of applying the plant phenological index technique, as proposed by West and Wein (1971) and Phillips (1976, 1980), to seagrass beds. Keddy and Patriquin (1978) were able to observe the development of flowering eelgrass shoots with such an index, but they distinguished only the most advanced development stages. However, such a method means a simplification, for it neglects the spatial differences described above, in the phenology of flowering shoots, which are caused directly or indirectly by the irradiance the plants receive and possibly also by temperature. This also applies for the temporal differences, which are expressed by differences in initiation time of shoots, branches and spathes and consequently also by changes in amounts of available nutrients. The phenological index only seems to be useful in the description of reproductive phases over a broad latitudinal distance. However, detailed observations remain necessary for the study of the patterns of development.

The oil of the "Amoco Cadiz" spill reached Roscoff on 20 March 1978, and was only visible during the following weeks. During that time, especially at the boundaries of the eelgrass beds, the impact was noticeable some leaves of vegetative shoots were black and looked as if they were burnt, whereas in other leaves transparent parts were visible (Jacobs, 1980). However, these leaves were shed and the production continued normally. Apart from this short-term effect, no other damage to the eelgrass itself was observed, although Calder et al. (1978) showed that eelgrass at Portsall contained hydrocarbons originating from the "Amoco Cadiz" oil, albeit without visible damage. With the results presented here it can be concluded that, compared with data from literature, the oil of the "Amoco Cadiz" had no observable effects on the vegetative and generative production of *Zostera marina* at Roscoff.

ACKNOWLEDGEMENTS

We would like to thank Prof Dr J. Bergerard and all investigators of the Station Biologique at Roscoff for the hospitality. We acknowledge Prof. Dr. C den Hartog, Dr R.C. Phillips, Drs J.J W.M Brouns and Drs. A W A M. de Cock for critically reading the manuscript and Mr J.J A. Slippens for producing the drawings. This work was supported by the Shell Internationale Research Maatschappij

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Studies on Aquatic Vascular Plants
edited by J J Symoens S S Hooper & P Compere
Royal Botanical Society of Belgium Brussels
1982 pp 150-155

REPRODUCTIVE STRATEGIES OF TWO SEAGRASS SPECIES (*ZOSTERA MARINA* AND *Z NOLTII*) ALONG WEST EUROPEAN COASTS

BY

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SUMMARY – Reproductive strategies of two seagrasses (*Zostera marina* L and *Z noltii* Hornem) were analyzed by comparing reproduction, productivity and phenology in various types of habitat

Classification of the plants by reference to strategies along the r-K continuum, suggests that the annual *Zostera marina* is an r-strategist and the perennial *Z marina* a K-strategist *Z noltii* can behave as a K-strategist in a disturbed environment characteristic for r-selection

Application of the strategy concept proposed by Grime, meets some inconsequent results, due to a generalization of plant properties and environmental conditions The implications of Grime's approach to plant strategies for the classification of seagrass vegetations are discussed

INTRODUCTION

Seagrass meadows along the West European coasts are characterized by two species belonging to the genus *Zostera*, i.e *Zostera marina* L. (eelgrass) and *Z noltii* Hornem. Both species are widely distributed in the intertidal and subtidal environments of nearly all the countries from the Norwegian Atlantic coast and the Baltic coast of Sweden and Finland in the north, to the coast of Portugal and Spain in the south However, the extreme limits of the distribution areas of the two species do not fully coincide . *Z noltii* has not been found in the Baltic (HUITEN 1971), and except for an old record of *Z. marina* in Algeria (see DEN HARTOG 1970), it seems to be the only *Zostera* species along the northern coast of Africa (LE GRAND 1969) Besides their distribution in coastal waters both species occur in marine and brackish inland waters in Denmark, The Netherlands and France

The seagrasses are adapted to an environment characterized by variations in a broad spectrum of abiotic factors The populations in the intertidal belt are particularly subjected to a quickly changing environment During the alternating high and low water periods the abiotic conditions differ considerably, e.g temperature, irradiation, salinity and the supply of nutrients. These changes are most clearly expressed along the Atlantic coasts of Europe, where extreme low water occurs at about midday and midnight, in contrast to the Wadden

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Sea where the extreme low tides occur in the morning and in the evening. In addition, seagrass populations occur under permanently submerged conditions with chlorinities ranging from minimum values of 2.7 ‰ [*Z. marina* along the Swedish east coast (WALLENTINUS 1979)] to temporary maximum values of 22-32 ‰ [*Z. noltii* at Corsica, France (VERHOEVEN 1980)]. These different and rather unpredictable habitats apparently favour the rapidly growing *Zostera* plants. In general adaptations to these environmental dynamics are expressed by high productivity, high turnover (MCROY & MCMILLAN 1977, JACOBS 1979) and, under certain conditions, also a high reproductive activity (NIENHUIS & DE BREE 1977, DE COCK 1981).

For several years *Zostera* meadows have been studied under a range of environmental conditions. At a number of study sites the productivity, phenology, reproduction and the seasonal changes in biomass were investigated in detail. A survey of these date is presented here, augmented by data from literature, in order to reflect on life-strategies of the two *Zostera* species.

LIFE-STRATEGIES OF THE TWO *ZOSTERA* SPECIES

ZOSTERA NOLTII

This small seagrass is widely distributed on intertidal flats. It occurs mainly in the area between the levels of mean high water neap (MHWN) and mean low water neap (MLWN) on bottoms with a high organic content (JACOBS & HUISMAN 1982). It commonly inhabits small and gently sloping elevations of the bottom surface. However, *Z. noltii* also occurs as a permanently submerged species in brackish waters along the Mediterranean coasts and in Denmark.

Z. noltii shows several regenerative characteristics in its life-time. Overwintering occurs by means of rhizome fragments, by scattered, very small shoots and by seeds. These seeds are of minor importance for the propagation of the species : seedlings are very rarely found in spring. The perennial rhizomes produce shoots throughout the year, with maximum numbers in spring and summer resulting in a relatively high above- and below-ground biomass during that period. The rather quick increase in biomass in early summer is a consequence of vegetative expansion of the rapidly growing rhizomes which branch monopodially and more or less continuously. In the intertidal belt the species is usually characterized by a high reproductive effort. During autumn and winter most of the populations are reduced due to heavy grazing by waterfowl, resulting in a negligible biomass in the early spring (JACOBS *et al.* 1981). Taking this into account, it seems reasonable that prior to a thorough study of the annual cycle, this seagrass has frequently been considered an annual plant.

ZOSTERA MARINA

Z. marina inhabits intertidal and subtidal areas on more or less sheltered places with muddy or sandy substrates. It occurs in fully marine waters, but also in the more or less stable brackish water of the Baltic and in some brackish inland lakes and ponds.

In the sublittoral and in the mid and lower intertidal regions *Z marina* appears to be a perennial plant characterized by the following life-strategies The plants produce leaves and rhizome-segments during all seasons but maximally in spring and summer (JACOBS 1979) Apart from this lengthening of the rhizomes the vegetative expansion is maximal in spring when the rhizomes branch diffusely and produce new lateral shoots This vegetative growth results in a mostly thick rhizome mat with a relatively high biomass, consequently creating a pool of reserve energy Sexual reproduction by means of flowering shoots is commonly little or absent (JACOBS & PIERSON 1981) and of minor importance because seeds are easily carried outside the potential distribution area by water currents

In the brackish inland waters along the Atlantic coast as well as in the upper parts of the eulittoral distribution area *Z marina* behaves as an annual plant In the intertidal region this annual seagrass grows in the depressions in the *Z noltii* meadows As an annual *Z marina* exhibits several characteristic life-strategies aimed at rapid completion of the life cycle and seasonal regeneration After germination of the seeds in spring and early summer nearly all energy is expended in the growth of flowering shoots which eventually become quite large This generative reproduction results in enormous quantities of seeds As these seeds are produced at places where currents are less marked the majority remain at the sites of production Hence *Z marina* is able to occupy more or less the same area each year Vegetative expansion by means of a more or less continuously branching rhizome is limited The function of the rhizome seems to be restricted to anchorage This results in a relatively low below-ground biomass

APPLICATION OF THE THEORY OF r- AND K SELECTION

In the theory about life histories and strategies proposed by MACARTHUR & WILSON (1967) and expanded by PIANKA (1970) plants can be designed along the r-K continuum in order to summarize the adaptations to environmental factors Towards one end of the continuum are the organisms of the r-type They are characterized by a short lifetime and use a large proportion of their resources for reproduction The other type, K-selected, consists of organisms from a more predictable environment They have a long life expectancy and are characterized by more periods of reproduction Generally these plants use only a small part of their resources for generative reproduction

Applying the r K selection theory to West European seagrasses *Z marina* when annual is an r-strategist a rapidly growing essentially annual plant using all its resources for flowering and *Z marina* when perennial is a K-strategist It thus appears that different populations belonging to the same seagrass species can occupy different positions along the continuum As both forms are genetically identical and can be grown from seeds of both (KEDDY & PATRIQUIN 1978 GAGNON *et al* 1980) the differences in life-strategies are responses of the same genetic pool to different environmental circumstances

Z noltii exhibits all strategies of either extreme on the r-K continuum It is a perennial plant which uses a large proportion of its resources for maintenance via rhizomes and roots and in that respect it is a K-stragegist However taking into account the less predictable environment in the higher littoral belt this seagrass contradicts the theory prediction by growing in an environment characteristic for r-selection

It can be concluded that both species take intermediate positions along the continuum, only the extremes of which are exactly defined Moreover, by the intraspecific variation in life-strategies application of the concept of MacArthur and co-workers appears useless, unless it is possible to quantify the reproductive effort of the plant populations For this it is not only necessary to consider the regenerative effort, as show by HARRISON (1979), but also to quantify the strategies in the established phase

APPLICATION OF THE CONCEPT OF STRATEGIES AS PROPOSED BY GRIME (1979)

Recently GRIME (1974 1979) presented a new theory concerning the concept of plant strategies He attributed two factors to the limitation of the amount of plant material fixed in populations i e stress and disturbance He defined stress as the external constraints which limit the rate of dry matter production of all or part of the vegetation and disturbance consists of the mechanisms which limit the plant biomass by causing its partial or total destruction As combinations of different levels of these factors compose the ultimate influence on populations, Grime distinguished three distinct types of primary strategies in the established phase

- competitors, i e plants which exploit conditions of low stress and low disturbance ,
- stress-tolerators, i e plants under influence of high stress and low disturbance
- ruderals, i e plants under influence of low stress and high disturbance

The primary strategies are defined very vaguely yet in spite of this they are extremes The vague description hinders definition of intermediate forms although Grime proposed four main types of secondary strategy, i e competitive ruderals (C-R) stress-tolerant ruderals (S-R) stress-tolerant competitors (C-S) and C-S-R strategists

In an attempt to classify the *Zostera* species according to the criteria used to define the strategies, recognition of key characteristics proved difficult The concept of strategy emphasizes the species as a population and as a unity with an active role in exploiting the habitat, consequently in competition with other populations In the case of the two *Zostera* species the stands are nearly always monospecific So, the relative importance of competition with regard to vegetation structure is negligible However, according to Grime the competitors are defined as species selected by conditions of low stress and low disturbance As these factors may also influence single-species stands, this approach accentuates the inherent intraspecific competition which has to be avoided when examining strategies determining the species composition of whole vegetations On the other hand it can be argued that the occurrence of monospecific stands results from a high competitive ability of the species However the seagrasses are the only vascular plants exploiting the sandy and muddy substrates in the marine environment, and the spatial segregation of species in the established phase seems to be more related to habitat conditions than to competition

In an attempt to classify the *Zostera* species according to Grime s descriptions of the different strategies the following types were distinguished

- *Zostera noltii* stress-tolerant ruderal
- *Zostera marina* (perennial) stress-tolerator
- *Zostera marina* (annual) ruderal

In order to relate strategy and life-form Grime introduced a triangular model based on two plant characteristics i e the "morphology index (calculated with data on leaf canopy, lateral spread etc) and the relative growth rate Based on this approach to classification the *Zostera* species do not fit completely in the above described patterns of strategy

- *Zostera noltii* stress-tolerant ruderal
- *Zostera marina* (perennial) competitor
- *Zostera marina* (annual) competitive ruderal

Comparison of these data must lead to the following conclusions Competitive ability is a plant characteristic that cannot be derived from monospecific stands Moreover, qualification after calculations with data on plant morphology seems to be useless without observations in habitats with mixed vegetations An additional fact is the intraspecific variation in life-strategies The difference between the two *Z marina* forms is associated with specific circumstances and reflects the highly plastic growth-responses of the species, but prevents the recognition of a well-defined main adaptive strategy However the employment of several strategies enlarges the capacity of the species to occur under a range of circumstances thereby widening its ecological range and may be considered to represent a strategy in itself

Thus, prior to a good understanding of strategies, observations should be made at plant level instead of at vegetation level, i e collecting autecological information about the ecological amplitudes This approach is recommended and a practical example is given by VERHOEVEN *et al* (1982) in these Proceedings

ACKNOWLEDGEMENTS

I should like to thank Prof Dr C den Hartog for constructive comments on the manuscript and Connie A N van Oorschot for correcting the English text

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Aquatic Botany, 8 (1980) 355—370
Elsevier Scientific Publishing Company, Amsterdam — Printed in The Netherlands

THE ANNUAL PATTERN OF THE DIATOMS IN THE EPIPHYTON OF EELGRASS (*ZOSTERA MARINA* L.) AT ROSCOFF, FRANCE

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(Accepted 4 February 1980)

ABSTRACT

Jacobs, R.P.W.M. and Noten, T.M.P.A., 1980. The annual pattern of the diatoms in the epiphyton of eelgrass (*Zostera marina* L.) at Roscoff, France. *Aquat. Bot.*, 8: 355—370.

The epiphytic diatom flora living on eelgrass, *Zostera marina* L., at Roscoff (France) has been observed during a whole year, from March 1976 to March 1977. The structure of this epiphyton has been analysed by investigating the species richness and the relative abundance of the taxa concerned. The study recorded 199 diatom taxa, representing 48 genera.

The epiphytic diatom association is characterized by *Cocconeis scutellum* Ehrenb., *C. scutellum* var. *parva* Grun. in Cleve and *Synedra investiens* W.Sm., of which *C. scutellum* and its variety are dominant throughout the year.

Differences in community structure between the diatom assemblages in the spring, summer, autumn and winter were most distinct as a consequence of the ephemeral character of the substrate. It appears that chlorine content and temperature have no direct effect on the species richness of the diatom association on eelgrass leaves. The seasonal variation in the epiphyton seems to be more closely related to insolation patterns and characteristics of the substrate and this relationship is discussed.

INTRODUCTION

Seagrass ecosystems are widely distributed and are among the most productive in the oceans (McRoy and McMillan, 1977). A seagrass meadow has a very complex structure (den Hartog, 1979), in which the seagrass itself is both the most important element and the most important primary producer (McRoy and McMillan, 1977; den Hartog, 1977). The other components of the ecosystem, which take part in primary production are benthic algae, phytoplankton and the epiphytic algae on the leaves.

It has been established that the epiphytes are important contributors to the total primary production of the community, sometimes amounting to 22% of the production of seagrass (Jones, 1968; Marshall, 1970; Penhale, 1977). In addition, it is possible that the production of the epiphytes is sustained by

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0304-3770/80/0000—0000/$ 02.25

nutrients released by their hosts (Harlin, 1971, 1973; McRoy and Goering, 1974). In contrast, Goering and Parker (1972) showed that the soluble nitrate excreted by blue-green epiphytic algae on the seagrass *Thalassia testudinum* Banks ex König is used by the host. All these relations have been demonstrated in experiments with representatives of the Rhodophyta, Phaeophyta and Cyanophyta, although it appears from scanning electron micrographs made by Sieburth and Thomas (1973) that diatoms of the genus *Cocconeis* are the first colonisers. These diatoms are very important from a functional point of view, because they reduce the photosynthetic rate of the leaves by acting both as a barrier to carbon uptake and by reducing light intensity (Sand-Jensen, 1977). Moreover, it is obvious that the diatoms (apart from carbonate-depositing red algae) are the most important structural elements of the epiphyton, for they take the greatest share in the epiphytic biomass.

The structure of the epiphyton on seagrasses and the relationships with the hosts were reviewed and discussed by Harlin in 1975, and more recently, in 1980. Most studies on the structure of the epiphytic vegetation of seagrasses concern the Rhodophyta, Phaeophyta, Chlorophyta and Cyanophyta (e.g. Brown, 1962; van den Ende and Haage, 1963; Humm, 1964; van der Ben, 1969; Ballantine, 1973; Brauner, 1975; Ballantine and Humm, 1975; Bird et al., 1976). In only a limited number of reports have the diatoms on seagrasses been described, e.g. in studies by Kita and Harada (1962), Dodd (1966), Edsbagge (1966), Reyes-Vasquez (1970), Main and McIntire (1974) and DeFelice and Lynts (1978), whereas Giffen (1970, 1976), during an inventory of the littoral diatoms of South Africa, has noted the epiphytic species of *Zostera capensis* Setch. The majority of these papers are reports of only short-term investigations.

The object of this work was to study the structure and species richness of the epiphytic diatom vegetation on eelgrass (*Zostera marina* L.) over a whole year. The data for other epiphytic algae and the cover of all epiphytes in relation to the age and the position of the eelgrass leaves will be published at a later date.

LOCALITY AND METHODS

This study was carried out at Roscoff, which is located on the North coast of Brittany (France), in an eelgrass bed situated ca. 3 m above the mean low spring water level (MLWS). A detailed description of the study area and the extent of the eelgrass meadows has been given by Joubin (1909), de Beauchamp (1914), Blois et al. (1961) and Jacobs (1979).

Samples were taken at irregular intervals, from March 1976 to March 1977, by cutting off eelgrass shoots with leaf blades of ca. 30—40 cm length, which were then taken to the laboratory. From each sample, the oldest leaf (commonly the fifth) was separated from the shoot and preserved immediately by fixing in 4% formalin in seawater. For analysis, the whole leaf was scraped off and after oxydation of the organic matter the empty frustules were mounted in Clearax. For each sample, a list of diatom taxa was recorded, after which the abundance of the different taxa was estimated by giving them the follow-

ing relative values: 1 = rare; 2 = common; 3 = very common and 4 = abundant. The most prominent taxa were selected by excluding taxa which scored less than a total of five points during the whole investigation period. No distinction was made between living cells and dead frustules. The taxa were identified with the aid of works by van Heurck (1896), Peragallo and Peragallo (1897—1908), Hustedt (1927—1960), van der Werff and Huls (1957—1974), Hendey (1964) and Pankow (1976), while the check-list of Hendey (1974) was followed for nomenclature.

Temperature data, insolation and chlorophyll content of the phytoplankton (see Fig. 1) were derived from the Laboratoire de Institut Scientifique et Technique des Pêches Maritimes (I.S.T.P.M.) de Roscoff and refer to station "NW. Batz", situated approximately 3.5 km from the study site (see Grall and Jacques, 1964).

RESULTS

Altogether, 199 diatom taxa (species and varieties) were found, representing 48 genera and belonging to 15 families (Table I). Approximately 50% of these taxa are obligately epiphytic, including species and varieties of the genera *Cocconeis*, *Licmophora*, *Achnanthes*, *Melosira* and *Synedra* (McIntire and Moore, 1977). In addition, tube-forming species of *Navicula* and *Amphipleura rutilans* and species of *Navicula*, *Nitzschia* and *Amphora* that form masses of cells within a gelatinous matrix can also be considered as real epiphytes (Main and McIntire, 1974). The other taxa represent planktonic diatoms (see Table I) and diatoms from epipsammic, epilithic and epipelic assemblages, which are entrapped among the other epiphytic algae on the *Zostera* leaves.

An attempt has been made to classify the diatoms on the basis of salinity data. For this purpose, the simplified categories proposed by Carpelan (1978) have been used, i.e. freshwater stenobiontic,† freshwater eurybiontic (oligohaline), mesohaline, holeuryhaline, marine eurybiontic (polyhaline) and marine stenobiontic (marine) (see Table I). The rather confusing variety of terms used in the literature have been altered to conform to these categories for as many taxa as possible. For 20% of the total number of taxa this was impossible because of a lack of adequate information in the literature. Although the taxa on *Zostera marina* represent diatoms from all categories, it appears that the most numerous are the eurybiontic organisms (approximately 70%), which have high tolerances to a broad variety of life conditions.

The total number of taxa found in each sample is given in Fig. 1. It appears that the number of taxa increased rapidly, from 26 at the beginning of March to a maximum of 74 in May, after which it decreased to 53 taxa at the beginning of July. After a new maximum in August (71 taxa) the number of taxa slowly decreased during autumn and winter. The decrease of the number of taxa in June—July coincided with a decrease in insolation (Fig. 1).

†Carpelan (1978) used the suffix '-topic', but we prefer '-biontic', because it implies independence of spatial distribution.

TABLE I

Diatom taxa found in the epiphyton of *Zostera marina* at Roscoff, France (figures indicate categories proposed by Carpelan (1978)

Taxa		Category
Class Bacillariophyceae		
Order Bacillariales		
Fam. Melosiraceae		
Melosira granulata (Ehrenb.) Ralfs ex Pritch.		2
Paralia sulcata (Ehrenb.) Cleve		5
Endictya oceanica Ehrenb.	(P)	5
Podosira stelliger (Bail.) Mann	(P)	5
Fam. Thalassiosiraceae		
Stephanodiscus astraea (Ehrenb.) Grun.	(P)	2
Cyclotella comta (Ehrenb.) Kütz.		2
Cyclotella stelligera Cleve		2
Cyclotella striata (Kütz.) Grun.		3
Thalassiosira excentrica (Ehrenb.) Cleve	(P)	5
Fam. Coscinodiscaceae		
Coscinodiscus heteroporus Ehrenb.	(P)	5
Coscinodiscus lacustris Grun. in Cleve and Grun.	(P)	6
Coscinodiscus lineatus Ehrenb.	(P)	5
Coscinodiscus nitidus Greg.	(P)	5
Coscinodiscus radiatus Ehrenb.	(P)	5
Coscinodiscus sp.		
Fam. Actinodiscaceae		
Actinoptychus senarius Ehrenb.	(P)	5
Fam. Eupodiscaceae		
Actinocyclus subtilis (Greg.) Ralfs ex Pritch.	(P)	5
Fam. Biddulphiaceae		
Biddulphia alternans (Bail.) Van Heurck		4
Isthmia enervis Ehrenb.		6
Fragilaria virescens Ralfs var. *subsalina* Grun.		2
Fam. Diatomacea (cont.)		
Glyphodesmis distans (Greg.) Grun.		5
Cymatosira belgica Grun.		5
Plagiogramma brockmannii Hust.		5
Plagiogramma gregorianum Grev.		
Plagiogramma vanheurckii Grun.		
Grammatophora angulosa Ehrenb.		5
Grammatophora marina (Lyngb.) Kütz.		5
Grammatophora oceanica Ehrenb.		5
Grammatophora oceanica var. *macilenta* (W.Sm.) Grun.		5
Grammatophora serpentina Ehrenb.		5
Rhabdonema arcuatum (Lyngb.) Kütz.		5
Rhabdonema minutum Kütz.		5
Rhaphoneis amphiceros Ehrenb.		5
Rhaphoneis nitida (Greg.) Grun.		5
Rhaphoneis surirella (Ehrenb.) Grun.		5
Denticula subtilis Grun.		4
Denticula tenuis Kütz.		2
Diatoma elongatum (Lyngb.) Agardh		3
Fam. Eunotiaceae		
Eunotia sp.		
Fam. Achnanthaceae		
Achnanthes brevipes Agardh		4
Achnanthes brevipes var. *intermedia* Kütz.		4
Achnanthes brevipes var. *parvula* (Kütz.) Cleve		4
Achnanthes delicatula (Kütz.) Grun. in Cleve and Grun.		4
Achnanthes hauckiana Grun.		4
Achnanthes lanceolata (De Bréb.) Grun.		3

Fam. Diatomaceae

Fragilaria capucina Desmaz.		2
Fragilaria capucina var. *lanceolata* Grun. ex Van Heurck		2
Fragilaria construens (Ehrenb.) Grun.		2
Fragilaria construens var. *subsalina* Hust.		2
Fragilaria hyalina (Kütz.) Grun.		5
Fragilaria intermedia Grun. ex Van Heurck		2
Fragilaria oceanica Cleve		5
Fragilaria pinnata Cleve		2
Fragilaria virescens Ralfs var. *subsalina* Grun.		
Opephora marina (Greg.) Petit		5
Opephora martyi Hérib.		3
Opephora pacifica (Grun.) Petit		5
Synedra fulgens (Grev.) W.Sm.		5
Synedra gaillonii (Bory) Ehrenb.		5
Synedra investiens W.Sm.		5
Synedra pulchella Kütz.		4
Synedra tabulata (Agardh) Kütz. var. *acuminata* Grun.		4
Synedra tabulata var. *fasciculata* (Kütz.) Grun.		4
Synedra tabulata var. *obtusa* Pantosek		4
Synedra tabulata var. *parva* (Kütz.) Grun.		4
Synedra ulna (Nitzsch) Ehrenb.		3
Thalassionema nitzschioides Hust.	(P)	5
Licmophora abbreviata Agardh		5
Licmophora anglica (Kütz.) Grun.		5
Licmophora communis (Heib.) Grun.		5
Licmophora ehrenbergii (Kütz.) Grun. var. *grunowii* (Mereschk.) Hust.		5
Licmophora gracilis (Ehrenb.) Grun.		5
Licmophora hyalina (Kütz.) Grun.		5
Licmophora juergensii Agardh		5
Licmophora lyngbyei (Kütz.) Grun. ex Van Heurck		
Licmophora paradoxa (Lyngb.) Agardh		5
Striatella delicatula (Kütz.) Grun. ex Van Heurck		5
Striatella unipunctata (Lyngb.) Agardh		5
Dimerogramma minor (Greg.) Ralfs ex Pritch.		5
Achnanthes lanceolata var. *elliptica* Cleve		3
Achnanthes lanceolata var. *rostrata* (Ostenf.) Hust.		3
Achnanthes longipes Agardh		5
Cocconeis californica Grun.		
Cocconeis clandestina Schm.		5
Cocconeis costata Greg.		5
Cocconeis dirupta Greg.		5
Cocconeis disculus (Schum.) Cleve		2
Cocconeis disculoides Hust.		5
Cocconeis distans Greg.		
Cocconeis fluminensis (Grun.) Perag.		
Cocconeis c.f. *lyra* Schm.		
Cocconeis molesta Kütz. var. *crucifera* Grun.		5
ex Van Heurck		2
Cocconeis pediculus Ehrenb.		3
Cocconeis placentula Ehrenb.		
Cocconeis placentula var. *euglypta* (Ehrenb.) Cleve		3
Cocconeis placentula var. *intermedia* (Hér. and Per.) Cleve		3
Cocconeis pseudomarginata Greg.		5
Cocconeis scutellum Ehrenb.		5
Cocconeis scutellum var. *minutissima* Grun.		5
Cocconeis scutellum var. *parva* Grun. in Cleve		3
Cocconeis stauroneiformis (Van Heurck) Okune		5
Rhoicosphenia curvata (Kütz.) Grun.		3
Campyloneis grevillei (W.Sm.) Grun.		4

Fam. Naviculaceae

Navicula abrupta (Greg.) Cleve		5
Navicula atlantica Schm.		
Navicula cincta Ehrenb.		3
Navicula crucifera Grun.		4
Navicula cryptocephala Kütz.		4
Navicula c.f. *cryptolyra* Brockm.		4
Navicula digito-radiata (Greg.) Ralfs		4

TABLE I (*continued*)

Taxa	Category
Fam Naviculaceae (cont)	
Navicula diserta Hust.	4
Navicula distans (W Sm.) Cleve	
Navicula flanatica Grun.	
Navicula forcipata Grev.	5
Navicula forcipata var. *densistriata* Schm.	5
Navicula gracilis Ehrenb.	2
Navicula gracilis var. *schizonemoides* Van Heurck	2
Navicula grevilleana Hendey	
Navicula halophila (Grun.) Cleve	4
Navicula henneavi W Sm	5
Navicula palpetralis De Bréb. in W.Sm.	5
Navicula pennata Schm.	
Navicula phylleota Kutz.	
Navicula ramosissima (Agardh) Cleve	5
Navicula rhynchocephala Kutz.	2
Navicula rostellata Kutz	2
Navicula rotaeana (Rab.) Grun.	2
Navicula salinarum Grun.	4
Navicula viridula Kutz.	2
Navicula sp	
Stauroneis amphioxys Greg.	4
Diploneis aestuarii Hust.	
Diploneis coffaeiformis (Schm.) Cleve	
Diploneis crabro Ehrenb.	5
Diploneis incurvata (Greg.) Cleve	5
Diploneis litoralis (Donk.) Cleve	5
Diploneis papula (Schm.) Cleve var *constricta* Hust.	5
Diploneis smithii (De Bréb.) Cleve	5
Diploneis splendida (Greg) Cleve	
Diploneis stroemii Hust.	5

Taxa	Category
Fam. Cymbellaceae (cont.)	
Amphora ovalis Kutz.	2
Amphora proteus Greg.	5
Amphora pusilla Greg.	
Amphora pusio Cleve	
Amphora salina W.Sm.	4
Amphora veneta Kutz.	2
Amphora sp.	
Cymbella cymbiformis (Agardh) Van Heurck	
Cymbella sp.	
Fam. Gomphonemaceae	
Gomphonema acuminatum Ehrenb.	1
Gomphonema exiguum Kutz.	5
Gomphonema olivaceum (Lyngb.) Kutz.	2
Gomphonema parvulum (Kutz.) Grun.	4
Gomphonema sp.	
Fam. Epithemiaceae	
Rhopalodia gibba (Ehrenb.) Müll.	2
Rhopalodia gibba var. *ventricosa* (Kutz) Grun.	2
Rhopalodia musculus (Kutz.) Mull.	6
Fam. Nitzschiaceae	
Nitzschia acuminata (W.Sm) Cleve in Cleve and Grun.	5
Nitzschia affinis Grun.	
Nitzschia angularis W.Sm.	5
Nitzschia c.f. *commutata* Grun.	4
Nitzschia denticula Grun.	2
Nitzschia dissipata (Kutz.) Grun.	2
Nitzschia frustulum (Kutz.) Grun. in Cleve and Grun.	3
Nitzschia hungarica Grun	3

Diploneis weissflogii (Schm.) Cleve	
Caloneis liber (W. Sm.) Cleve	5
Trachyneis aspera (Ehrenb.) Cleve	5
Trachyneis aspera var. *intermedia* (Grun.) Cleve	5
Trachyneis aspera var. *pulchella* (W. Sm.) Cleve	5
Mastogloia pusilla Grun.	
Amphipleura rutilans (Trent.) Cleve	3
Pleurosigma angulatum (Quekett) W.Sm.	
Pleurosigma formosum W.Sm.	
Pleurosigma lanceolatum Donk.	5
Pleurosigma marinum Donk.	5
Gyrosigma spencerii (W.Sm.) Cleve	4
Gyrosigma subsalinum Perag.	
Fam. Cymbellaceae	
Amphora coffeaeformis (Agardh) Kütz	5
Amphora exigua Greg.	5
Amphora c.f. *macilenta* Greg.	5
Amphora marina W.Sm.	6
Amphora ostrearia De Bréb. var. *lineata* Cleve	5
Nitzschia lanceolata W.Sm.	4
Nitzschia microcephala Grun. in Cleve and Grun.	
Nitzschia palea (Kütz.) W.Sm.	3
Nitzschia panduriformis Greg.	5
Nitzschia panduriformis var. *minor* Grun.	5
Nitzschia pseudofonticola Hust.	
Nitzschia punctata (W.Sm.) Grun.	
Nitzschia punctata var. *coarctata* Grun.	
Nitzschia sigma (Kütz.) W.Sm.	4
Nitzschia socialis Greg.	
Nitzschia vitrea Norman	4
Nitzschia sp. 1	
Nitzschia sp. 2	
Hantzschia amphioxys (Ehrenb.) Grun.	2
Fam. Surirellaceae	
Surirella armoricana Perag.	
Surirella fastuosa Ehrenb.	4
Surirella ovata Kütz.	2
Surirella ovata var. *pinnata* (W.Sm.) Hust.	2

(1) = freshwater stenobiontic (= freshwater); (2) = freshwater eurybiontic (= oligohaline); (3) = freshwater to marine (= mesohaline); (4) = freshwater to hyperhaline (= holeuryhaline); (5) = marine eurybiontic (= polyhaline); (6) = marine stenobiontic (= marine); (P) = planktonic taxon.

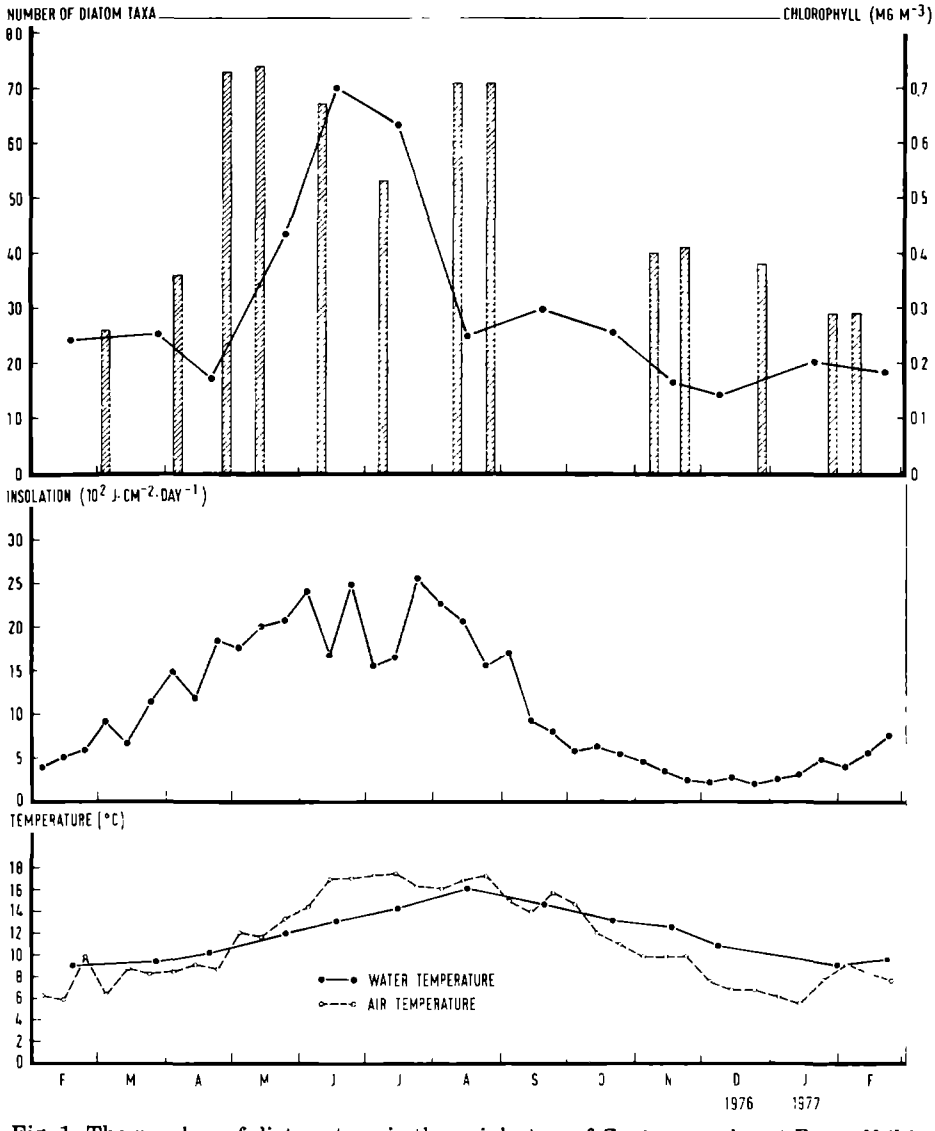

Fig. 1. The number of diatom taxa in the epiphyton of *Zostera marina* at Roscoff (histograms) and the chlorophyll content of the phytoplankton (line) compared with insolation and temperature in the period from February 1976 till March 1977. The air temperature and insolation are given as mean values per 10-day period.

After selection of the most prominent taxa, the resulting list was composed of 61 taxa (see Table II). To obtain a better survey these taxa were arranged in Table II in such a way that the floristic composition of the epiphytic vegetation became easily recognizable, with a group of taxa characteristic for the epiphytic assemblage during the whole year and three other groups which were more abundant during a particular season.

The diatom vegetation on *Zostera marina* was predominantly composed of *Cocconeis scutellum*, *C. scutellum* var. *parva* and *Synedra investiens*. *Cocconeis scutellum* and its variety were present during all seasons and were especially abundant in the autumn and winter. These diatoms were fixed with one valve on the substrate surface and formed a crust layer, which was always accompanied by *S. investiens*. This diatom formed short ribbons on eelgrass throughout the entire year, although it was less common during summer. Taxa associated with the characteristic vegetation were as follows: *Cocconeis scutellum* var. *minutissima*, *Synedra gaillonii*, *S. tabulata* var. *fasciculata*, *Grammatophora oceanica* var. *macilenta*, *G. marina*, *Fragilaria hyalina*, *Navicula flanatica*, *N. diserta* and *Paralia sulcata* (see Table II).

Ten taxa were only abundant in the association during spring: two taxa were restricted to this period, while the other ones were occasionally recorded in other seasons too. The most conspicuous taxa which could be regarded to be characteristic of the spring were: *Navicula cincta*, *Rhoicosphenia curvata*, *Nitzschia affinis*, *Licmophora juergensii*, *Fragilaria construens*, *F. oceanica* and *Achnanthes brevipes* var. *parvula*.

During the summer the epiphytic diatom association contained both more taxa and more taxa exclusively found in these months. This group consisted of about twenty taxa with *Cocconeis molesta* var. *crucifera* and *C. stauroneiformis* as the most common ones, as shown in Table II.

The composition of the epiphytic vegetation during autumn and winter was less diverse than in other seasons, with only 4 characteristic taxa, of which *Synedra tabulata* var. *obtusa*, *Cocconeis placentula* var. *euglypta* and *Eunotia* sp. were common (Table II).

DISCUSSION

Intertidal and estuarine ecosystems are very complex and are characterized by both chemical and physical gradients. As the distribution of marine algae is primarily controlled by four abiotic factors, i.e. light, temperature, salinity and water movement (Gessner and Schramm, 1971), the ranges of tolerance to these factors have to be determined along these gradients. Several authors have tried to categorize diatoms on the basis of salinity data and used a refined 'Halobien' system (e.g. Hustedt, 1953, 1957; van der Werff and Huls, 1957—1974; Simonsen, 1962; Pankow, 1976). However, they have neglected the ranges of tolerance that should be considered in changing aquatic environments. At Roscoff, many environmental factors are variable and subject to unpredictable changes. At high tide, a strong flood current exists along the coast. Because of this supply of ocean water, the chlorinity is nearly constant throughout the year (19.4‰) and water temperature changes only gradually, with minimum values of 9°C in February and maximum values of 16°C in August (Anonymous, 1976) (see Fig. 1). Emersion during low tide results in considerable changes of environmental characteristics of the eulittoral zone, especially during summer, when the water temperature in intertidal pools

TABLE II

Seasonal variation in the occurrence of the most prominent diatom taxa in the epiphyton of *Zostera marina*

Species	Occurrence						
Cocconeis scut. var. minutissima		2	3	2	2	3	
Synedra gaillonii	1	2	2	2	2	3	3
Grammatophora oc.var. macilenta	3	2	2	2	2		3
Fragilaria hyalina	3	3	3	3	3	1	2
Cocconeis scutellum	4	3	3	3	3	2	2
Cocconeis scut var. parva	3	4	3	3	3	3	3
Synedra investiens	2	3	3	2	2	1	1
Grammatophora marina	2	1	2	2		3	2
Synedra tab. var. fasciculata	1	3	1	1			3
Navicula flanatica	1	2	2	2	2	2	3
Navicula diserta		1	1	2	2	2	1
Paralia sulcata		1	1	1	1	1	3
Coscinodiscus lineatus	1	1	1	1	1		
Achnanthes hauckiana	1		2	1	2	1	
Amphipleura rutilans			3	3			
Navicula cincta		2	2	2	1		
Rhoicosphenia curvata	1	1	2	2	1	1	
Nitzschia affinis	1	2	2	1	2	1	1
Licmophora juergensii	3	2	2	2	1		1
Fragilaria construens	1	3	3	2	2		1
Achnanthes brev. var parvula	1	2	3	3	3		
Fragilaria oceanica	3	3	2	2	2	1	
Navicula cryptocephala			1	2	1	1	1
Achnanthes longipes		1		1		1	
Diploneis aestuarii		1	1	1			1
Navicula forcipata			1	1	1		
Synedra pulchella	1		1		1		
Coscinodiscus sp		1	1			1	1
Navicula forc. var. densistriata			1	1			1
Navicula rhynchocephala			2		1		
Nitzschia sp. 2			2		2		
Synedra tab. var. parva			1	1			1
Navicula salinarum			1		2		
Trachyneis aspera	1			1	2		
Rhaphoneis nitida				1		1	2
Rhaphoneis amphiceros				1	1	1	1
Biddulphia alternans				1	1	1	1
Nitzschia panduriformis				1	1	1	1
Navicula halophila				1		1	2
Gomphonema exiguum			2		2	2	
Cocconeis placentula			1	2	2		2
Licmophora hyalina				1	1	1	1
Synedra tab. var. acuminata			2	2	1	2	
Amphora exigua				2	2		1
Pleurosigma lanceolatum				2	2		1
Trachyneis asp. var. pulchella			1		2	1	2
Navicula gracilis			1	2	1	1	2
Amphora veneta				2	2	1	2
Striatella delicatula		1				3	3
Cocconeis mol. var. crucifera			1		3	2	2
Cocconeis stauroneiformis			1	2	3	2	3
Grammatophora oceanica						2	
Podosira stelliger			1		1	1	1
Achnanthes brev. var. intermedia			1				2
Striatella unipunctata						1	2
Rhabdonema arcuatum							2
Licmophora abbreviata						1	1
Thalassionema nitzschioides				1			1
Cocconeis plac var. euglypta				1		2	
Synedra tab var. obtusa							
Eunotia sp.							
Date	040376	060476	300476	140576	110676	090776	130876

at Roscoff (1 = rare; 2 = common; 3 = very common; 4 = abundant)

2	2	2	2	1	
2	1				
3					
1	1				3
3	4	4	4	4	4
3	3	4	4	4	4
2	2	2	2	2	3
3	1	1	1		2
3	1	2	2	2	
3	1	2		2	
1	3	2	2	2	
2	1	1	1	1	1
		1	1		
	1	2			1
			1		1
	1	1	1		1
1					
1	1			1	1
1				1	2
	1				
	1	1		1	1
1		1	1		
		1			
	2	1			1
1					2
				1	1
			1	1	
1					1
		1			
2					
	1				
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2		1			
2					
2	1				
2		1		2	
2	1		1		
3	1				
3			1	1	
3	2	1			1
		1			2
1			1		
1		1	1		
3					
3					
3					
1	1	1	2		
	1	3	3	2	1
		2	2		1
	3	2	2	1	1
270876	101176	231176	281276	310177	100277

may increase (sometimes to 25°C), coinciding with conditions of supra-oceanic chlorinities inducing such effects as dehydration and desiccation. Conversely, periods of precipitation will temporarily cause sub-oceanic chlorinities in the littoral belt. All these short-term fluctuations influence the eelgrass community, a fact reflected by the occurrence of a large variety of diatoms from nearly all the categories described by Carpelan (1978) in the epiphyton; only stenobiontic species adapted for life in freshwater are absent (see Table I). Diatoms of the polyhaline class form 55% of the most common species recorded in Table II. According to Carpelan (1978) the eurybiontic character of these species permits them to colonize waters with unstable conditions, these species lack freshwater tolerance, but often have hyperhaline tolerance, and also a tolerance to temperature changes.

The genus *Cocconeis* was represented on plants of *Zostera marina* at Roscoff by 19 taxa, of which 7 appeared to be common (Tables I and II). These diatoms form a crust on the substrate, which can be regarded as a pioneer vegetation on the eelgrass leaves (Sieburth and Thomas, 1973). According to Edsbagge (1966), *Cocconeis* reaches its optimum development only on phanerogams and algae with flat thalli. He found representatives of this genus in Sweden not only on *Z marina*, but also on such algae as *Delesseria*, *Odonthalia* and *Phyllophora*. This is in agreement with the reports of Takano (1961, 1962), who found *Cocconeis scutellum* dominant on Gelidiaceae, *Sargassum* and *Cystophyllum*. On plants of *Zostera* at Roscoff, *C scutellum* and *C scutellum* var. *parva* were dominant throughout the entire year. This was also true of *C. scutellum* var *minutissima*, although this variety was less abundant than other species. *Cocconeis scutellum* has been regarded as a polyhaline species (see Table I). Edsbagge (1966) found this species on *Z. marina* in Sweden at a chlorinity of 13‰ , whereas Main and McIntire (1974) noted an occurrence at chlorinities from 8.8—18.7‰ .in Oregon (U.S.A.), illustrating the wide range of chlorinity tolerance which this species has.

According to salinity data given by Edsbagge (1966), *Cocconeis scutellum* var. *parva* has been classified as a mesohaline species. However, Edsbagge (1966) did not find this variety on *Zostera marina*, but on some Chlorophyta and Rhodophyta, and only along the southern part of the West coast of Sweden. He suggested that this diatom is more abundant along the other, more southern European coasts At Roscoff it was a characteristic species on *Z. marina*, with a maximum occurrence during the winter period (see Table II), and also in Oregon, U.S.A. (Main and McIntire, 1974). *Cocconeis placentula* was a less abundant species at Roscoff, and was only present on *Zostera* plants during summer. In the epiphyton of the seagrass *Thalassia testudinum*, this diatom was a dominant species (Reyes-Vasquez, 1970, DeFelice and Lynts, 1978) and most abundant during the late spring and early summer (Reyes-Vasquez, 1970) at chlorinities of 16.7—21.4‰ *Cocconeis placentula* has been regarded as a mesohaline species, with a tolerance extending into freshwater. This is confirmed by the results of Catteano and Kalff (1978) and Eminson (1978), who found *C placentula* dominant respectively on *Potamogeton*

richardsonii (A. Benn.) Rydb. and *Myriophyllum spicatum* L.

The diatoms in the epiphyton of *Zostera* concern not only the specimens found on the eelgrass itself, but also those on the other algae attached to this substrate. The epiphytic vegetation lives on an ephemeral substrate; eelgrass shoots are characterized by a continuous production of new leaves, the oldest ones being shed regularly. New leaves on a shoot appear between the older ones and are protected by them. They grow primarily in the basal region (Sand-Jensen, 1975) during ±3 plastochrone intervals, (P.I. i.e. the time interval between the initiation of two successive leaves on a shoot), (Tomlinson, 1974; Jacobs, 1979). Hence, the distal parts of the leaves are the oldest parts and become colonized at first by recruitment from the adjacent leaves, the epipelon, the epipsammon, the epilithon and the plankton. After a period of ±3 P.I.'s the eelgrass leaves are fully developed and the epiphytes have expanded their coverage over almost the entire leaf blade. For this investigation, the oldest leaves, i.e. the fourth or fifth leaf on a shoot, have been used. Thus, it is reasonable to conclude that the epiphytic vegetation on that leaf substratum had reached maximum development and was not older than 5 P.I.'s.

Another aspect of the substratum influenced the variability in the epiphytic vegetation, the variation in plastochrone interval during the year. It appeared that the course of the P.I. showed a striking and reverse correlation with insolation, with a minimum P.I. of 13 days in May and a maximum value in December (±28 days). The average P.I. concerning the whole observation period was 19.3 days (Jacobs, 1979). This meant an average turnover time, i.e. an average lifetime of leaves, of 97 days for shoots with five leaves (ranging from 67 days in May to 140 days in December). Thus, the average lifetime of the epiphyton on an eelgrass leaf was also restricted to 97 days.

It is apparent from the preceding discussion that the influence of a particular environmental factor on the distribution of the epiphyton differs from day to day. Nevertheless, there are seasonal trends in these factors, and these are reflected in variations in the epiphyton and also in the phytoplankton, as shown in Fig. 1. The curve of the chlorophyll concentration of the phytoplankton at Roscoff with a first bloom in June, followed by a second smaller one in September (Fig. 1) shows the same seasonal trends as the theoretical cycle described by Riley (1946) and Davis (1955). According to Grall and Jacques (1964), this cycle is primarily controlled at Roscoff by the amount of light. However, the number of diatom taxa in the epiphyton of *Zostera marina*, although possibly a dubious parameter in comparison with the number of diatom cells, shows a deviating course, suggesting another ecological factor controlling the epiphyton. It appears that the seasonal trend in the epiphyton coincides with patterns in insolation (Fig. 1) and eelgrass production given by Jacobs (1979). Taking into account the direct nutrient relationship between eelgrass and its epiphyton, as shown by Harlin (1971, 1973), McRoy and Goering (1974) and Wetzel and Penhale (1979), low eelgrass productivity results in a lower richness in diatoms, i.e. in the months of June and July and during the winter of this investigation period. Hence, it is possible to conclude that the

richness of the epiphytic diatom vegetation of *Zostera marina* is directly correlated with the eelgrass productivity. In addition, the ephemeral nature of the substrate accentuates the differences in the epiphyton structure during the year.

Variations in the possible reducing effects of the epiphyton on the eelgrass photosynthesis, as found by Sand-Jensen (1977), were not detectable in this study, as these effects are approximately constant throughout the year. Moreover, direct effects on the eelgrass productivity are probably negligible, as the production of leaf tissue occurs only at the base of the first three leaves and these leaf parts are not covered with epiphytes.

ACKNOWLEDGEMENTS

We thank Peter Hermelink and Guido van Geel, who collected the samples at Roscoff, and members of the I.S.T.P.M. at Roscoff for the data on phytoplankton, temperature and insolation and Mr. J.J.A. Slippens, who made the drawing. We wish to express our appreciation to Prof. Dr. C. den Hartog, Prof. Dr. C. van den Hoek and Drs. G. van der Velde for reviewing the manuscript. Thanks are also due to Prof. Dr. J. Bergerard and the staff of the Station Biologique at Roscoff for the hospitality. This investigation has been financed by the Netherlands Organization for the Advancement of Pure Scientific Research (ZWO).

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EPIPHYTIC ALGAE ON EELGRASS AT ROSCOFF, FRANCE.

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ABSTRACT

Algae growing as epiphytes on eelgrass, Zostera marina L., at Roscoff, were investigated during one year by examining the species richness and abundance. The abundance of the algae, expressed as cover values, appeared to be influenced by the characteristics of the substrate, especially the ephemeral status and growth rate of the leaves.

Colonization of the seagrass leaves occurred primarily on tips and edges, subsequently spreading over the faces to the base. The pioneers appeared to be the dominant, persistent taxa, of which Audouinella virgatula (Harv.) Dixon, Fosliella lejolisii (Rosan.) Howe, Myrionema magnusii (Sauv.) Lois. and the diatoms were most prominent. The oldest parts of fully grown leaves showed the most diverse epiphytic vegetation. Though there was a form of succession, a climax community was not reached.

On examining the spatial distribution of the epiphytes, a group of characteristic taxa was seen to be accompanied by a second group, whose variation in occurrence seemed to be correlated with the height in the littoral.

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INTRODUCTION

Epiphytes are organisms which live on plants. Both faunal and algal species are found on seagrasses; a comprehensive list was compiled by Harlin (1980) in her review of seagrass epiphytes. In contrast to mobile epiphytic fauna, the life-span of the algae and the immobile animals is restricted to the life-time of the substrate, i.e. the seagrass leaves. The ephemeral character of this substrate is determined by external biological and physical factors, but also by internal physiological properties of the particular seagrass species itself. The maximum life-time of leaves of Posidonia oceanica (L.) Delile, near Calvi (Corsica), is more than one year (D. Bay, pers. comm.), whereas Jacobs (1979) measured 67 - 140 (average 97) days for leaves of Zostera marina L. at Roscoff (France). In contrast to these characteristics of perennial vegetations, other seagrass populations are only present in the established phase during part of the year (Wyer et al., 1977; Harrison, 1979; Jacobs, 1982). This places a high demand on the species epiphytizing the seagrasses, as colonization of the ephemeral substrate is only possible during the reproductive phase of the algae or, in the case of substratum specificity, the algae have to complete their whole life-cycle on the seagrasses. This last phenomenon consequently implies a higher turn-over rate of the epiphyte than that of the host.

Considering the abiotic environment of the epiphytes, physical phenomena can be assigned the most differentiating factors. Primarily, the seagrass leaves form a specific physical substrate, consequently restricting the potential number of epiphytic species by the surface tension of the host, as suggested by Linskens (1963). In addition, water motion and tidal currents cause a continuous movement of the narrow and weak seagrass leaves. As the leaves also constantly rub against one another, these substrates are unsuitable for algae characterized by a broad and/or long thallus. These algae are rarely found as young or small specimens, consequently not reaching a reproductive phase in their development. Other physical factors influencing the presence and distribution of algae are directly correlated with the depth distribution, i.e. the quantity and quality of available light (Hellebust, 1970), pressure (Van et al., 1976; Lloyd et al., 1977) and temperature.

The effects of all the environmental factors mentioned determine the ultimate species composition in a given habitat and the ultimate development of a more or less characteristic epiphytic vegetation. Such a vegetation was the subject of this study at Roscoff. Moreover, by examining the epiphytes in seagrass meadows at different depths and in relation to the age and position of the leaves, it was possible to investigate some influences separately, in addition to features such as colonization and succession.

STUDY AREA AND METHODS

Roscoff is a small town located on the north coast of Brittany (France). The area between the shore and Ile de Batz (an island situated one kilometre to the north of Roscoff) is characterized by extensive meadows of eelgrass, Zostera marina, both under eulittoral and sublittoral conditions. Detailed descriptions of the study area and the distribution of the seagrass have been given by Joubin (1909), De Beauchamp (1914), Blois et al. (1961) and Jacobs (1979). In recent years several aspects of this community were intensively studied, i.e. production, biomass and phenology of the plant community (Jacobs, 1979; Jacobs and Pierson, 1981), epiphytic diatoms (Jacobs and Noten, 1980) and the inhabiting macrofauna (Jacobs and Pierson, 1979; Jacobs, 1980; Den Hartog and Jacobs, 1980; Jacobs and Huisman, 1982).

The present investigation was carried out from April 1976 to March 1977, during which period the temperature and salinity of the seawater and the solar insolation were measured. These data were presented by Jacobs (1979) and Jacobs and Noten (1980).

For the study of the temporal pattern in the epiphytic vegetation, a sampling station was selected in an extensive, homogenous eelgrass bed just to the south of Ile Verte (see Jacobs, 1979). At each sampling date (see Table 1) two or three well-developed eelgrass shoots, each with a minimum of five leaves, were clipped, brought to the laboratory and immediately investigated. If necessary, the plants were preserved in 4% formalin in seawater. After Van der Ben (1971) the seagrass leaf blades were divided into 8 cm long sections, measured from the transition between leaf blade and leaf sheath. Eight centimetres was chosen to allow easy handling under the binocular. For each leaf-part epiphytic algae other than diatoms were listed, using the check-list by Parke and Dixon (1976) for the nomenclature. Subsequently the abundance of each species was estimated according to a modified Braun-Blanquet scale (Barkman et al., 1964), in which R = 1-3 scattered specimens, cover on average 0.3%; + = a few scattered specimens, cover on average 0.7%; 1 = many specimens, cover 1-5% (av. 3%); 2 = cover 5-20% (av. 12%); 3 = cover 20-40% (av. 30%); 4 = cover 40-70% (av. 55%); 5 = cover 70-100% (av. 85%). Subsequently data from corresponding leaf-parts were averaged. The composition and cover of the epiphytic community on the rim (edge) and the lamina (face) of the leaves showed conspicuous differences and were therefore separately estimated.

For an estimation of the spatial distribution of the epiphytic algae on Z. marina, samples were taken on 25th August at 14 stations at different heights in the littoral. Each sample was characterized by a species list and a rough estimate of the cover of the recorded algae according to: 1 = cover 0-10%, 2 = cover 10-40% and 3 = cover 40-100%.

RESULTS

TEMPORAL PATTERNS

The algae colonizing the leaves of Zostera marina form an association, which shows negligible differences in species richness and abundance between the leaf sides, but great differences in both temporal and spatial composition. Older leaves and flowering shoots are sometimes so heavily overgrown that eelgrass tissues are no longer visible. Frequently the total cover of epiphytes reaches values of more than 100% (see also Fig. 1). In some cases the linear form of the leaves is no longer recognizable, as tufts of algae with erect filaments or parenchymatous thalli, in addition to tube-forming Bacillariophyceae, cover them completely. Mainly in spring and autumn the occurrence and abundance of the algae show remarkable spatial differences, as mentioned by Den Hartog (1976). This appears to be

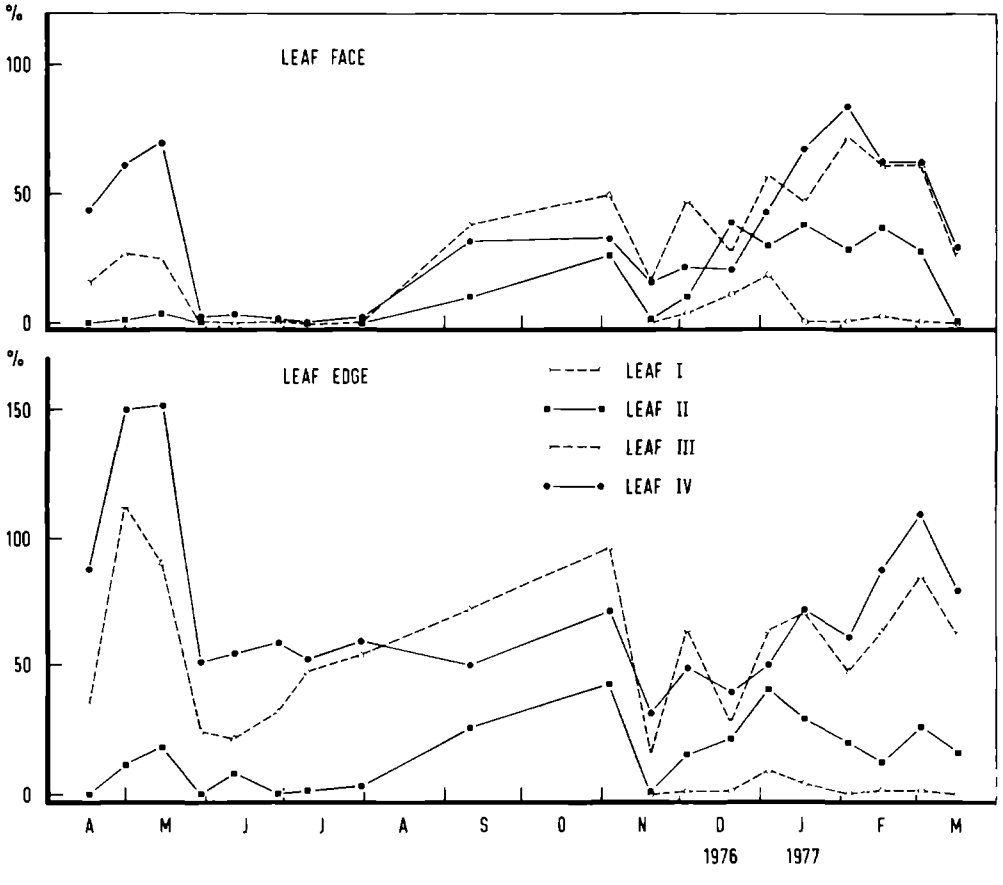

Fig. 1. Temporal patterns in the average total cover of epiphytic algae on faces and edges of Zostera marina leaves at Roscoff (the youngest leaf is indicated as I).

due to particular environmental conditions in different parts of the seagrass bed, creating suitable micro-habitat for development of characteristic algae. For instance, in spring this results in most luxurious local vegetations of Erythrotrichia spp. on only a few leaves, or Ectocarpaceae covering all shoots growing over several square metres. Consequently, such leaves may become so heavy that they are easily broken off by waves. Such a situation especially occurs during autumn storms and influences the standing crop of the seagrass profoundly, as shown by a significant lower average number of leaves per shoot (Jacobs, 1979).

In order to be able to inquire into possible seasonal trends in coverage of epiphytic algae, all relevés made of eelgrass leaves of a specific age (with leaf I as youngest) were grouped at each sampling date and an average total cover for the whole leaf was calculated. The resulting data with separate cover values for leaf face and leaf edge are shown in Fig. 1. When examining the trend in total cover values several remarkable phenomena can be noted:

- No algae occur on leaf sheaths;
- The leaf edges appear more covered with algae than the leaf faces;
- The abundance of algae on the youngest leaf is negligible in spring and summer, only reaching detectable quantities from November onwards, with highest covers in December and January;
- On both leaf faces and leaf edges the cover increases from the younger to the oldest leaves. However, the third leaves appear more densely populated than the fourth in the period from September to December;
- After a period with very high cover values in May, lower values are recorded in June and July, especially for the leaf faces. After a gradual increase in cover to the beginning of November, the subsequent values appear to fluctuate.

The algae found as epiphytes on Zostera marina at the sampling station south of Ile Verte are listed in Table 1, in addition to the total number of relevés investigated. However, some remarks have to be made on the taxa mentioned in this Table. A detailed report on the Bacillariophyceae, including a list of species, was published in 1980 by Jacobs and Noten. Ectocarpus spp. included only two species, E. fasciculatus Harv. and E. siliculosus (Dillw.) Lyngb., which in most cases could not be distinguished due to an absence of sporangia. A comparable situation may be assigned to the records of Punctaria sp. As Punctaria tenuissima (C. Ag.) Grev. was found on neighbouring substrates, which were less ephemeral than the seagrass leaves, the epiphytic Punctaria was probably the same species. Asperococcus spp. included probably two species, i.e. A. fistulosus (Huds.) Hook. and A. turneri (Sm.) Hook. The classification and systematics of the Cyanophyceae are very confused (e.g. Parke and Dixon, 1968, 1976; Drouet, 1968, 1973). Therefore, identification of the bluegreen algae based on incidentally found specimens did not seem justified. However, during winter Microcoleus lyngbyaceus (Kütz.) Crouan frat. ex Gom. and Calothrix crustacea Thur. ex Born. et Flah. could be identified, many specimens occurring on a few leaves. The remaining taxa, mentioned only with a genus name, were young, incidentally found algae, which could not be identified with certainty.

TABLE 1

Synoptic table of the relevés from the epiphytic community on Zostera marina during one year. Indications are given of frequency of occurrence on the leaf faces (higher figures) and the edges (lower figures); 1 - 5: frequency of occurrence in the relevés, 1 = 0-20%, 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%.

Date	16 Apr 1976	30 Apr	14 May	29 May	11 Jun	26 Jun	9 Jul	30 Jul	10 Sep	3 Nov	19 Nov	3 Dec	20 Dec	3 Jan 1977	17 Jan	3 Feb	16 Feb	2 Mar	16 Mar
Species																			
Acrochaetium virgatulum (Harv.) Nixon (R) x	1/4	3/5	2/5	1/4	4/4	1/4	5/5	5/5	4/5	2/5	3/5	4/5	4/5	4/5	4/5	4/5	4/5	3/5	3/4
Acrochaetium sp.	1/4	1/2	3/4	2/3	1/4	1/3	1/2	1/2	2/4	4/5	2/4	5/5	5/4	5/5	4/5	5/5	5/5	5/5	4/4
Antithamnion boreale (Rosenv.) Howe (R)	4/4	4/5	3/4	1/3	1/2	2/3	1/3	1/2	3/3	2/4	4/5	5/5	2/4	5/5	5/5	5/4	5/4	3/3	3/3
Bacillariophyceae	3/3	3/3	3/4	2/4	2/4	2/3	1/3	1/2	3/3	1/2	1/2	2/2	3/5	3/3	5/5	4/3	4/2	4/2	3/3
Myriotrichia filiformis Harv. (P)	1/1	1/1	1/2	1/2	2/2	1/2	1/3	2/2	3/3	1/2	1/1	1/1	1/1	1/1	2/2	1/2	1/1	1/2	1/2
Erythrotrichia bertholdii Batt. (R)	2/2	2/3	2/2	1/2	2/2	1/2	1/2	1/2	1/2	1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
Heterocarpus spp. (P)	2/2	3/3	2/2	1/3	1/3	1/2	1/2	1/2	1/2	1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
Ceramium rubrum (Huds.) C. Ag. (R)	1/1	1/1	1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	2/1	1/1	2/1	1/1	1/1	1/1	1/1
Erythrotrichia borgesen (Mont.) Berth. (R)		1/2	1/2	1/3	3/3	3/3	3/3	2/2	1/1	1/1	2/2	1/1	1/1	1/1	1/1	1/1	1/1	1/2	1/2
Cyanophyceae								1/1			1/1				1/1	1/1	1/1	1/1	1/1
Elothrix flacca (Dillw.) Thur. in Le Jol (C)	2/1	3/3	1/1								1/1				1/1	1/1	1/1	1/1	1/1
Erythrotrichia carnea (Dillw.) J. Ag. (R)	1/1	1/4		1/3	1				1/2		1/1								
Pilayella sp. (P)	1/1	1/1	1/1	1/1		1/1					1/1					1/1		1/1	1/1
Elothrix subflaccida Wille (C)	1/1	2/2																1/1	1/1
Crop yeast spp. (young)		1	1/1										1/1			1/1	1/1		
Asperococcus sp. (P)	1/1	1/1	1/1	1/1			1/1												
Polysiphonia sp. (R)				1/1		1/1		1/1			1/1								
Monostroma sp. (L)				1		1/1			1/1									1/1	1/1
Myriotrichia clavaeformis Harv. (P)					1/1	1/1	1/1	1/1										1/1	1/1
Phaeophila viridis (Reinke) Burrows (C)									1/1	1/1	1/1								
Enteromorpha sp. (C)					1/1														
Porphyra sp. (R)																		1/1	
Number of relevés	49	65	68	69	50	62	68	67	47	26	67	49	47	37	46	44	63	36	43

x (= Chlorophyceae; P = Phaeophyceae, R = Rhodophyceae

The persistent taxa on the eelgrass leaves showed remarkable differences in abundance in the course of the year (see Table 1) with lower numbers toward the end of spring and beginning of summer, especially with respect to the leaf faces. This temporary decrease was previously noticed by Jacobs and Noten (1980) for the Bacillariophyceae. Comparing the results presented in Fig. 1 and Table 1, it can be concluded that the epiphytes were not only present during this period in lower abundance, but also in a lower number of relevés.

The first seven taxa mentioned in Table 1, i.e. Audouinella virgatula, Fosliella lejolisii, Bacillariophyceae, Myrionema magnusii, Erythrotrichia bertholdii, Ectocarpus spp. and Ceramium rubrum, were found on all the eelgrass shoots sampled, although for some species only one or a few specimens were found during winter. Other species, such as Erythrotrichia boryana, E. carnea, Punctaria sp., Ulothrix spp. and Asperococcus spp., appeared more or less restricted to the months March to June, whereas Myriotrichia clavaeformis and Phaeophila viridis were only recorded in summer.

Comparing the presence data for leaf faces and leaf edges, most taxa were more frequently found on the edges, suggesting a colonization from the edge towards the middle of the leaves. However, encrusting algae, i.e. Fosliella lejolisii, Myrionema magnusii, and also the diatoms belonging to the genus Cocconeis, were occasionally more abundant on the leaf faces.

COLONIZATION AND SUCCESSION

Two factors primarily determine the initial colonization of seagrass leaves by algae, i.e. the presence of reproductive stages for potential colonization and the suitability of the leaves as substrate. The combination of both factors continuously influences the actual species composition and abundance of epiphytes. The ultimate composition of the epiphytic association is directly related to the growth characteristics of the seagrass, which as a consequence of a constant production of new leaves and a loss of the oldest is an ephemeral substrate. New leaves on a shoot appear between the older ones by which they are protected. They grow primarily from the base (Sand-Jensen, 1975; Jacobs, 1979), the tip being the oldest part of a leaf. Leaves grow during a period of 58 days on average, with a minimum of 39 days in May and a maximum of 84 days in December. The average life-time of leaves on shoots with five leaves ranges from 67 to 140 days (average 97 days) (Jacobs, 1979). This ephemeral character of the seagrass requires a continuous colonization of the new leaves by recruitment from adjacent older leaves or from other substrates. Differences in age exist both between the leaves of a single shoot and the tip and base of a single leaf. Inherent to these differences is the possible investigation of epiphytic association on a single shoot, at both a pioneer stage and all subsequent developmental stages, i.e. the succession of the association. Hence, seagrass as a substrate is eminently suited to studies on the phenomenon of succession. What the final stage will be, is predominantly determined by the life-span of the substrate. As this

varies with the season, the development of the association will be described together with examples of estimations in summer and winter for the dominant taxa (Fig. 2).

Initial colonization occurs usually on the second leaf of the shoots (see also Fig. 1), though due to high growth rates in summer this leaf sometimes remains uncovered or shows only a few epiphytes on the tip. Several characteristics can be noted:

- The pioneers appear to be the dominant, persistent taxa (see Table 1), accompanied on older leaves by Erythrotichia bertholdii with mostly low cover values.
- Colonization of the leaves always occurs from the tip to the base and from the edge spreading over the face, consequently accompanied by a decreasing cover. However, Myrionema magnusii and the Bacillariophyceae sometimes appear to form an exception by showing a higher cover on the face than on the edge (e.g. Fig. 2b). The ultimate cover appears to be strongly dependent on the growth rate of the substrate: a high growth rate sometimes results in a lower cover and/or an absence of certain algae on the leaf face (Audouinella virgatula and Fosliella lejolisii in Fig. 2a).
- The oldest part of fully grown leaves is considered the optimal place for settlement and development of the other taxa, resulting in a very diverse epiphytic vegetation on the leaf tips. This sometimes concurs with a decreasing cover of Audouinella virgatula, Fosliella lejolisii and Erythrotrichia boryana (Fig. 2).

SPATIAL DISTRIBUTION

Near Roscoff Zostera marina is distributed from mean low water mark at neap tide (MLWN) down to a depth of 4 metres below the mean low water mark at spring tide (MLWS). As the subtidal eelgrass meadows are almost unattainable due to strong currents, the study on the spatial distribution of the epiphytes has been carried out in the littoral, extending a difference in height of approximately 3 metres. On 25th August 14 selected stations were sampled and species richness and abundance of the epiphytes on the eelgrass were estimated. It should be noted that the results presented here only apply to the date in August and are not representative for other seasons.

The first seven taxa in Table 2 (Bacillariophyceae, Myrionema magnusii, Audouinella virgatula, Fosliella lejolisii, Ceramium rubrum, Polysiphonia c.f. violacea and Ectocarpus c.f. siliculosus) were recorded on all sampled seagrass shoots and appeared to form a combination of species characteristic for the epiphytic association. However, this association represents only the situation in August, as on a yearly basis the composition of the group of characteristic species shows some variation (compare with Table 1). The total number of taxa found at the different stations ranged from 10 to 14, and due to differences in species composition, the total list of taxa for all stations (without the Bacillariophyceae) amounted to 27.

In addition to the characteristic taxa a group of companion taxa can be distinguished, which is separately indicated in Table 2. The variation in occurrence of these taxa seems to be correlated with the

TABLE 2

Spatial distribution of the epiphytes of Zostera marina at Roscoff on 25th August. Sampling stations 1 - 4 were situated at MLWN (mean low water mark at neap tide), the stations 12 - 14 at LLWS (low low water mark at spring tide) and the others at intermediate levels of gradually increasing depth (1 = cover up to 10%; 2 = cover 10-40%; 3 = cover 40-100%).
Note the occurrence of three distinguishable groups: characteristic taxa, companion taxa and incidental inhabitants.

Sampling station	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Height above LLWS (m)	3.0	3 0	3.0	3 0	2.4	2.2	2.1	2.1	2.1	2 1	1.8	0.3	0.2	0.2
Number of Taxa	11	10	13	11	11	12	10	11	11	12	10	10	13	14
Taxa														
Bacillariophyceae	1	1	1	1	2	2	2	2	1	2	2	1	2	2
Myrionema magnusii (Sauv.) Lois. (P)*	3	3	3	3	3	3	2	2	3	3	3	3	3	2
Audouinella virgatula (Harv.) Dixon (R)	3	3	3	3	3	1	2	3	3	3	3	1	3	3
Fosliella lejolisii (Rosan.) Howe (R)	2	2	1	1	2	3	3	3	1	1	3	3	3	3
Ceramium rubrum (Huds.) C. Ag. (R)	2	2	1	1	1	1	2	3	1	3	1		1	1
Polysiphonia c.f. violacea (Roth) Spreng (R)	1	1	1	1	1	1	2	2	1	1	1	1	1	1
Ectocarpus c f siliculosus (Dillw.) Lyngb (P)	2	1	2	2	3	2	3	3	1	3		2	2	1
Calothrix crustacea Thur. ex Born et Flah (Cy)	1	1	1											
Pringsheimiella scutata (Reinke) Marchew (Chl)			1	1										
Ectocarpus sp (P)	2	1	1	1	1	1	2	2						
Erythrotrichia carnea (Dillw.) J. Ag. (R)	1	1	1	1	1	1	1	2	1	1				
Enteromorpha sp (Chl)			1	1	1	1	1	2	1	2				
Chylocladia verticillata (Lightf.) Bliding (R)			1		1	1		1						
Erythrotrichia berthold11 Batt. (R)				1				1	1	1	2	1	2	3
Champia parvula (C. Ag.) Harv. (R)											1	1	1	1
Erythrotrichia boryana (Mont.) Berth. (R)											1		1	3
Ectocarpus c f fasciculatus Harv. (P)													3	2
Asperococcus turneri (Sm.) Hook. (P)	1				1	1					1	1		
Polysiphonia c f. urceolata (Lightf. ex Dillw.) Grev (R)						1								
Myriotrichia clavaeformis Harv. (P)							1		1					
Asperococcus fistulosus (Huds.) Hook. (P)											1			1
Ulva sp. (Chl)														1
Asparagopsis armata Harv (R)									1					2
Microcoleus sp (Cy)										1				
Punctaria tenuissima (C Ag.) Grev. (P)										1				
Antithamnion spirographidis Schiffner (P)												1		
Hypoglossum woodwardii Kutz. (R)													1	
Polysiphonia insidiosa Crouan frat. (R)														1

* Chl = Chlorophyceae, Cy = Cyanophyceae; P = Phaeophyceae; R = Rhodophyceae

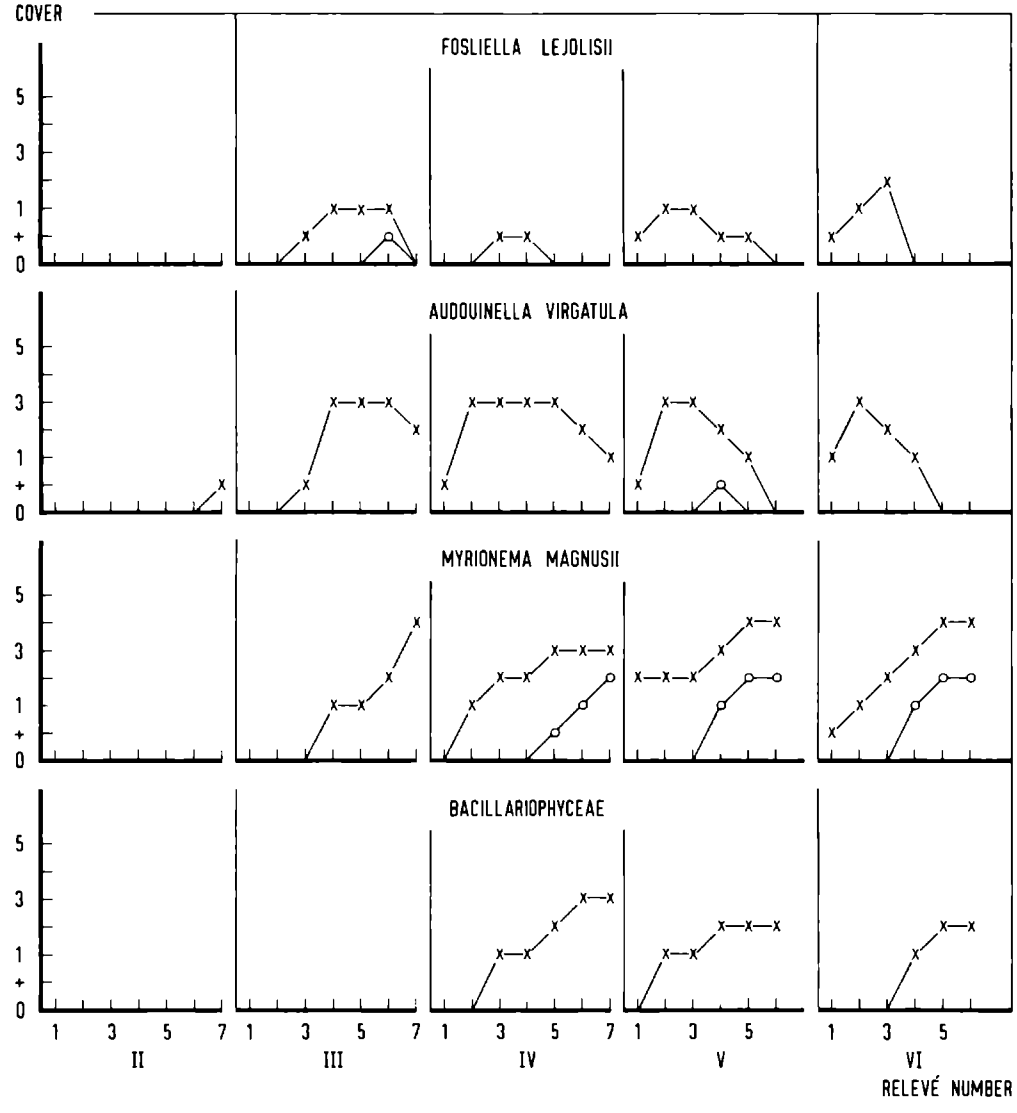

Fig. 2a. Cover of the dominant epiphytic taxa on leaf faces (circles) and edges (crosses) of Zostera marina shoots, sampled on 28th June (left) and 16th February (right). The cover (for the explanation of the symbols see text) was estimated on the different leaves (Roman numerals), which were each divided in sections of 8 cm length (Arabic numerals).

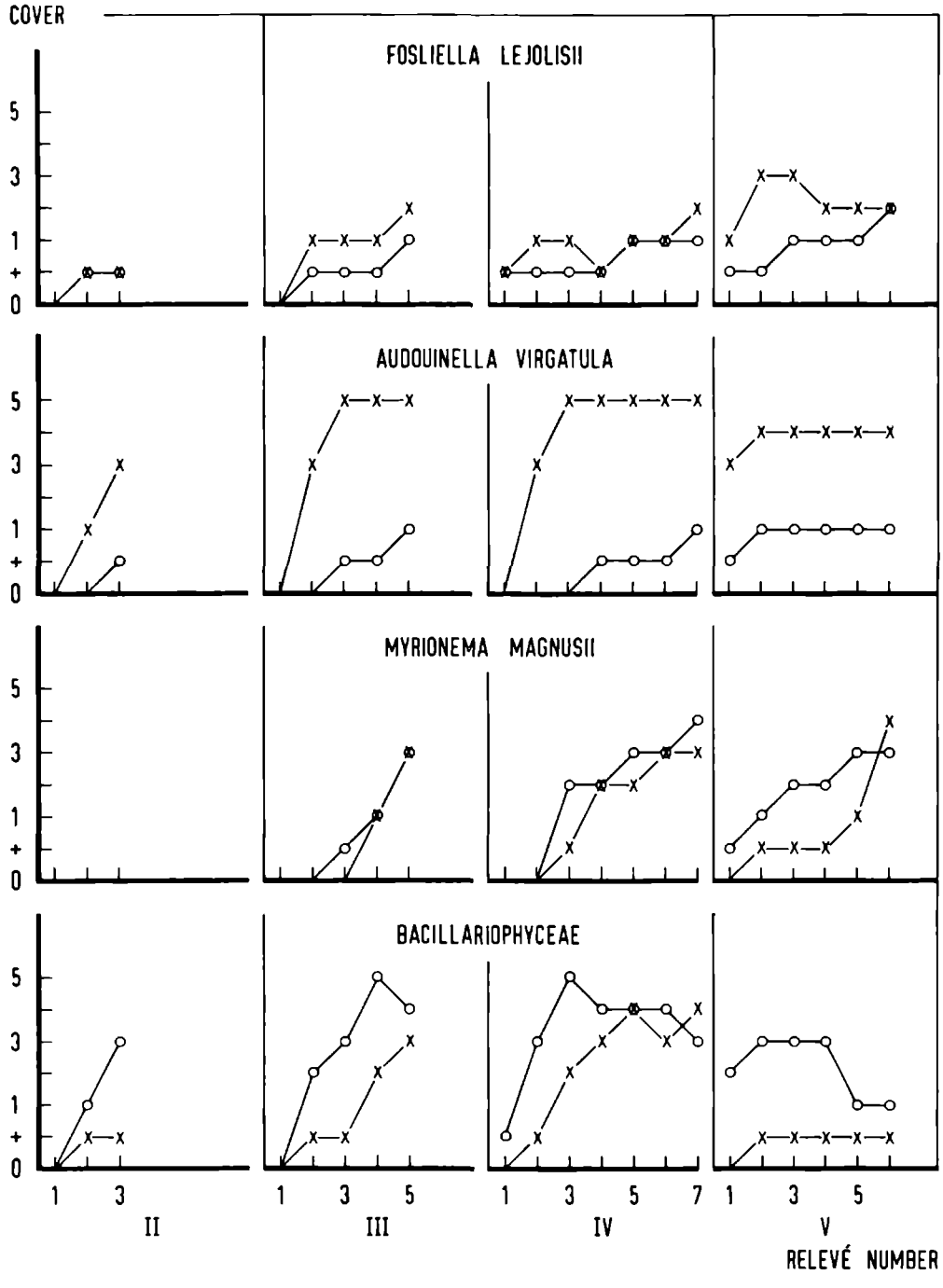

Fig. 2b. See legend on facing page.

height in the littoral. Comparing the higher and lower situated beds, the algae of this group show a shift to more red algae with higher cover values towards the lower situated sampling stations. The third group of algae comprises the incidental inhabitants, found in only one or two samples and never reaching high cover values.

Seagrass on places which are strongly exposed to tidal currents (e.g. stations 6 and 12 in Table 2), shows a somewhat deviating epiphytic vegetation. The difference is only expressed by the abundance of the species. The encrusting algae appear most common and reach an optimum development both on the leaf faces and edges. Other algae are present, but without a high cover. Though establishment does take place, longer erect thalli are apparently easily broken off and the ultimate vegetation structure differs considerably from that in less exposed areas.

DISCUSSION AND CONCLUSIONS

Many epiphytic macro-algae on Zostera have been listed in specific reports on the host (see Davis, 1913; Brown, 1962; Van den Ende and Haage, 1963; Hargraves, 1965; Harlin, 1971; Brauner, 1975), as well as in handbooks and floras (e.g. for Western Europe: Hamel, 1924-1930, 1930-1932, 1931-1939; Newton, 1931; Hamel and Lemoine, 1952; Feldmann, 1954, 1964; Cardinal, 1964; Kuckuck, 1964; Pankow, 1971; Dixon and Irvine, 1977). However, the distribution and the position of the epiphytes on the eelgrass shoots in relation to the age of the leaves was only studied by Van den Ende and Haage (1963). They found that at Roscoff the young leaves show a higher density of epiphytes near the leaf base. On mature leaves the density increased to the leaf tip with a subapical maximum concentration in a zone 20 - 30 cm above the leaf base. These results are contradicted by the patterns described and illustrated (Fig. 2) in this study: with a few exceptions practically all species showed a maximum cover at the tip of the leaves. In view of the growth characteristics of the shoot and the relationship between leaf length and leaf age (see Jacobs, 1979, Fig. 3), the maximum cover would be expected at the leaf apex. In our opinion a possible explanation for the deviating results reported by Van den Ende and Haage (1963) may be the effects of gastropods grazing the epiphytic vegetation. We observed numbers of gastropods of 100 - 200 per m^2 (approximately 12 species) with an overall dominance (about 75% of the total numbers) of Gibbula cineraria (L.) and G. pennanti (Philippi). It was only possible to observe the grazing behaviour of these animals during low water periods. During that time the seagrass shoots were lying flat on the bottom surface in a few centimetres of water. Only about 10% of the gastropods present appeared to graze actively on the outer side of the leaves, the remainder being found on the leaf sheaths and on other substrates between the shoots. The situation during the high water periods is not known, though grazing would seem impossible on waving leaves. Examination of leaves with trails left by gastropods, showed a non-selective grazing, leaving only the encrusting species. However, grazing was not restricted to the leaf apices, and as the grazing pressure was not equally distributed over

the meadows, this can only partially explain the deviating data given by Van den Ende and Haage (1963).

The epiphytic vegetation is seen to be eminently suited to studies on succession. Independent of the season, the same group of algae colonizes the bare leaves in the same way, i.e. the pioneer epiphytic community. Characteristic species of this group include diatoms belonging to the genus Cocconeis (Jacobs and Noten, 1980), which are considered to be the first colonizers (Sieburth and Thomas, 1973). The development of the pioneer community is rapid and influenced by a competition for space and light. The pioneers are partly replaced or overgrown by other algae during the life-time of the leaf. However, the vegetation continues to develop as the leaves mature and no stage of equilibrium seems to be reached during the life-time of an eelgrass leaf. This is a direct result of a non-simultaneous and non-uniform colonization of a single leaf. Therefore, though there is a form of succession, a climax community as a 'steady state' is not reached, and the final stage is determined by the age of the substrate and not by inter- and intraspecific processes between the epiphytes. The final stage can be considered a variant of the pioneer stage. Besides, the final community shows differences depending on the season and the life-span of the seagrass leaves in that season.

The colonization process is influenced by several phenomena which are directly related to the interaction between growth characteristics and responses to physical factors of both the seagrass and the epiphytes. As young seagrass leaves extend upwards between the older ones, the apices are first exposed to diaspores of epiphytes. When species are represented by mobile spores, they form potential epiphytes. However, only 'haptophytes' (Luther, 1949; Den Hartog and Segal, 1964) attach themselves to the seagrass leaves (Den Hartog, 1972). Horizontally growing, encrusting algae are successful colonizers, as distinct from plants attached by discs, basal cells or haptera, which mostly produce upright thalli. These algae are hampered in growth by adjacent older leaves on the same shoot, as a consequence of mechanical interactions, and therefore their occurrence is nearly restricted to leaf edges and older leaves. As the seagrass leaves grow vertically, all described features apply to both sides of the leaves, colonization patterns and species richness and abundance being comparable.

Examination of the development of the association for one year, shows a distinct periodicity expressed by temporal variations in cover (Fig. 1). This is a result of several coinciding factors, whose individual contributions cannot be distinguished clearly. The most important factors include:

- The life-span of the seagrass leaves. Variations in the 'plastochrone interval' (see Jacobs, 1979) determine the period available for establishment and colonization of the substrate.
- The period of algal propagation, i.e. the occurrence of free-living, reproductive stages of potential epiphytes.
- Environmental conditions, e.g. variation in salinity, temperature, insolation and available nutrients. These factors were discussed previously by Jacobs and Noten (1980) in relation to seasonal patterns in occurrence of epiphytic diatoms on Zostera marina.

- Damage of the substrate by waves (especially during autumn and winter) and of the epiphytic vegetation by grazing invertebrates.
- The physical and chemical characteristics of the substrate may contribute to a selection of the potential epiphytes.

In spite of all influences mentioned, the association, especially in the pioneer stage, was found in all the samples taken and may be regarded as an association characteristic for seagrass. A comparable association with more companion species was reported by Van der Ben (1971) for Posidonia oceanica in the Mediterranean. Other temporal variations concern the differences in species composition from year to year. For instance, Rhodophysema georgii Batt., mentioned by Den Hartog (1976) as a characteristic epiphyte of Zostera marina at Roscoff, was not found during this investigation, whereas the species was recorded both in 1978 and 1979 (pers. observation).

Several authors have mentioned the restriction of specific epiphytes to marine phanerogams, e.g. Myrionema magnusii (Feldmann, 1954; Loiseaux, 1967), Rhodophysema georgii (Feldmann, 1954; Den Hartog, 1976), Cladosiphon zosterae (J. Ag.) Kylin (Feldmann, 1954), Fosliella lejolisii (Suneson, 1943; Dawson, 1960; Masaki, 1968). Strictly speaking this is not correct, as some of these have been recorded from other substrates, e.g. Fosliella lejolisii from *Sargassum and other algae (Chamberlain, 1977; Coppejans, 1980).* However, in general these algae are mainly found in epiphytic communities on seagrasses and only incidentally on other substrates. The true Zostera epiphytes consist of a group of algae, which are also found on other seagrass species. However, on those seagrasses the characteristic epiphytes may be replaced or supplemented by species with a comparable habit or other species of the same genus. This last phenomenon may be illustrated by the genus Fosliella, which is widely distributed, e.g. Van der Ben (1971) found F. farinosa (Lamour.) Howe and F. lejolisii on Posidonia oceanica, and Humm (1964) recorded the same species on Thalassia testudinum Banks ex König. In her study on Fosliella, Chamberlain (1977) reported a rare occurrence of F. limitata (Foslie) Ganesan on Zostera marina near the Isle of Wight. In addition, she recently encountered a new species of Fosliella on Z. marina (Chamberlain, pers. comm.). As crusts of these species are almost indistinguishable without sectioning, it is not improbable that Fosliella species other than F. lejolisii may be present on the seagrasses near Roscoff.

ACKNOWLEDGEMENTS

We thank Prof. Dr. C. den Hartog and Prof. Dr. M. Vroman for critically reviewing the manuscript, Connie A.N. van Oorschot for correcting the English text, Mr. J.J.A. Slippens for the drawings, Theo Platel for preparing the tables and drawings, and Dora Williams for typing the manuscript. Thanks are also due to Prof. Dr. J. Bergerard and the staff of the Station Biologique at Roscoff for their hospitality. This investigation was financed by the Netherlands Organization for the Advancement of Pure Research (ZWO).

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Macrobenthos of some *Zostera* beds in the vicinity of Roscoff (France) with special reference to relations with community structure and environmental factors

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Communicated by Prof. V. Westhoff at the meeting of November 30, 1981

ABSTRACT

In the eulittoral area near Roscoff (France) several seagrass beds were studied, which were characterized by either *Zostera marina* L. or *Z. noltii* Hornem. In addition to faunal assemblages, the sediment structure and the floristic elements of the community were examined.

The species diversity of the macrofauna increased with the degree of water coverage (i.e. the percentage of time each contour is covered with water) and was correlated with the environmental stability and structural complexity of the community. The faunal similarity between the different sampling stations was rather low due to differences in sediment structure and the number and nature of micro-habitats present. Consequently there was a segregation of species for each separate structural element of the community.

The results of this study show that in order to arrive at a natural systematic classification of *Zostera* communities all structural elements of the community should be considered. The implications of these results are discussed

INTRODUCTION

Den Hartog (1979) distinguished 19 structural elements in seagrass communities. However, not all seagrass communities contain all these elements: structural complexity is linked to the dominant seagrass species. Communities characterized by species of the genus *Zostera* subgen. *Zosterella* have been considered to be the most simple. More differentiation can be found in communities dominated by species of the genus *Zostera* subgen. *Zostera* (Den Hartog, 1970, 1977). Apart from the seagrass itself (the frame of the community), other important structural elements are the benthic algal and faunistic components. The richness of the animal populations and the variety of organisms are directly

related to the presence of different habitats and food resources within the community. The faunal assemblage can be divided into several vertically arranged layers corresponding to the organization and presence of floristic elements of the seagrass bed, e.g. rhizome layer, mat of algae between the shoots, epiphytic algae on the leaves, etc. (Thayer & Phillips, 1977). Due to a more structural complexity the diversity and species richness are higher in an eelgrass (*Zostera marina* L.) bed than in neighbouring bare areas (Orth, 1973; Thayer et al., 1975). The fundamental structure and function of the faunal components of these communities seem to be similar in a variety of geographic regions (Kikuchi & Pérès, 1977; Kikuchi, 1980).

In order to explain fully the natural pattern of species abundance in eelgrass communities, several factors other than habitat complexity can be pointed out (see also Den Hartog, 1979) for which predation and competition are of importance. According to Menge & Sutherland (1976) the most important factor controlling the abundance at lower trophic levels in rocky intertidal

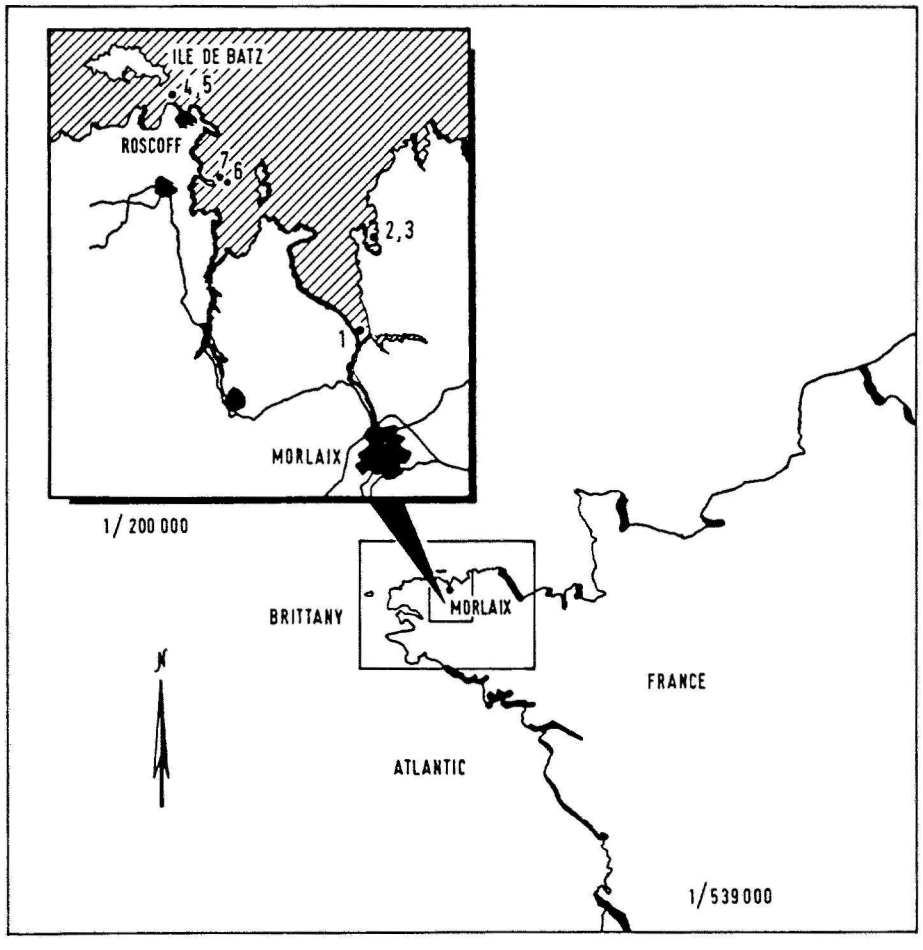

Fig. 1. Map of the Roscoff area, showing the location of the sampling stations.

communities is predation. Exclusion-cage experiments in seagrass beds showed a distinct effect of predation in regulating invertebrate abundance (Young et al., 1976; Young & Young, 1978; Reise, 1977, 1978; Nelson, 1979). However, physical factors also have to be known when comparing the structure of different seagrass communities. Sediment type, for instance, (Gray, 1974) and the depth distribution of the communities are of importance, governing distribution and diversity of the animals. Data from sediment infauna show an increasing diversity with increasing water depth (Johnson, 1970; Day et al., 1971).

The aim of this study has been to evaluate the most important factors controlling the structure and diversity of some *Zostera* communities, dominated by *Z. marina* L. (subgenus *Zostera*) and *Z. noltii* Hornem. (subgenus *Zosterella*). In order to come to an analysis, several apparently different *Zostera* beds in the vicinity of Roscoff were chosen, differences due to geographic latitude thus being excluded. An attempt was made to analyse floristic elements and environmental factors and to determine their relation to the patterns of species abundance in the faunal assemblages.

LOCALITIES AND METHODS

During May 1979 seven eulittoral stations – here arranged according to an increasing sandy sediment structure – were sampled in the vicinity of Roscoff (see Fig. 1):

1 a *Zostera noltii* Hornem. stand in the Bay of Morlaix near Locquénolé;
2 a *Z. noltii* stand in the Bay of Tenerez;
3 a *Z. marina* stand in the Bay of Tenerez: this seagrass was found in depressions or tidal pools (approximately 5–10 cm deep) in the *Z. noltii* bed where water was retained at low tide;
4 a *Z. marina* bed situated just to the south of Ile Verte (near the "Station Biologique" at Roscoff) (see also Jacobs, 1979a);
5 a *Z. marina* stand situated between Station 4 and the "Station Biologique" at Roscoff (see also Jacobs, 1979a);
6 a *Z. marina* bed in the Bay of Morlaix to the east of Ile St. Anne near Penpoul;
7 a *Z. noltii* stand in the Bay of Morlaix to the north-east of Ile St. Anne.

The mean number of seagrass shoots m^{-2} and the mean length of the shoots was determined at each sampling station and the abundance of epiphytic algae on the seagrass leaves was estimated. Likewise the presence or absence of a mat of algae between the shoots was noted. The height of the different seagrass beds in the littoral was estimated by comparison with adjacent algal stands, for which the standard zonation is given by Den Hartog (1959) and Lewis (1964).

At each station, several (on the average 6) bottom samples were taken randomly in the seagrass vegetation by handcoring, using PVC tubes (9.5 cm long and 2.5 cm diam). After mixing the subsamples the sediment material was dried for 24 hours at 105°C. Part of the dried material was combusted for 5 hours at 550°C to determine the ash-free dry weight, which is expressed as per-

centage of the dry weight. The ash-free dry weight equals the dry organic content, assuming that carbonates, bicarbonates and crystallic water were not decomposed (Vollenweider, 1969). Particle size analysis was carried out with a dried sample of 2–5 g. This was destructed with conc. H_2SO_4 under heating, after which the remaining carbon was oxidized with 30% H_2O_2. After washing several times by centrifugation, the sand fractions were determined by sieving through 200 μm and 50μm mesh. The remaining fraction of silt and clay was analysed with a Sartorius Sedimentation Balance 4610, using water as a sedimentation liquid. From the resulting weight/time diagram the weights of the different fractions were calculated. For this it was necessary to assume that all particles consisted of quartz and had a spherical shape.

The benthic fauna was sampled at each station by taking 6 random subsamples in the seagrass bed. This was carried out with a corer of 9 cm diam, which was driven into the bottom to a depth equal to the thickness of the rhizome mat. In the absence of a distinct mat, the samples were taken to a depth of approximately 10 cm. The animals retained by a 0.5 cm mesh sieve were preserved in 70% ethanol, sorted and identified.

Diversity indices were calculated from the data, i.e., Shannon's index, $H = -\Sigma_{i=1}^{S} P_i \ln P_i$, with P_i = proportion of the abundance of species i and S = number of species, and the evenness of H, namely $J = H/H_{max}$, where $H_{max} = \ln S$ (Pielou, 1969). Margalef's diversity index was calculated as $d = S-1/\ln N$, where N = number of individuals (Margalef, 1967).

The percentage faunal similarity in all pairs of stations was calculated according to the formula of Goodall (1973), $C = (2\Sigma \min.\ a_i\ b_i)/(\Sigma a_i + \Sigma b_i)$ where a_i and b_i are the numbers of individuals of the i'th species at the stations A and B respectively. For classification of the percentage similarity values the principle of Mountford (1962) was applied. From the table of indices of similarity the two highest values were selected and the data of the corresponding stations were combined to form a new, single group. The indices of similarity between this new group and each of the other stations were evaluated and a new reduced table was obtained. The index with the highest value in the reduced table was then selected and the procedure repeated.

The quantitative importance, i.e. the biological index (see Fager, 1957; Sanders, 1960), was determined by ranking the species from 1 to 5 by abundance in each subsample. A value of 5 points was given to the first ranking species, 4 points to the second ranking species, etc. Thus, if a species was ranked first in all 6 subsamples, it would have 30 points, the highest possible score, agreeing with 33.3% of the total number of points awarded per sample.

Dispersion pattern analysis was made for the 6 subsamples using the variance to mean ratio, or "index of dispersion". The departure from unity was assessed by reference to a table of χ^2 (Elliott, 1977).

RESULTS

DESCRIPTION OF THE FAUNAL ASSEMBLAGES: NUMERICAL ANALYSIS

Particle size distribution of the sediments at the different stations showed

great differences. In Table 1 the stations are arranged according to an increasing sand fraction and a decreasing fraction of silt and clay, concurring with a decreasing dry organic matter content of the bottom. Three types of sediments were distinguished:

1. silt with a high content of clay and a high organic content (Station 1);
2. sand with a high silt content and a relatively high organic content (Stations 2, 3 and 4);
3. sand with little silt and clay and a low organic content (Stations 5, 6 and 7).

All stations showed a well-sorted sediment, except Station 4.

The composition of the benthic faunal assemblages at the stations is given in the Tables 2 and 3. In these tables the totals of the numbers found in all 6 subsamples, taken at each station are indicated. The total number of species found was 85 and there were great differences in species composition between the different stations. The fauna also showed great variations in abundance (see Table 4): the mean numbers (± SE) of individuals per m^2 varied from 2384 (± 279) at Station 3 (minimum) to 18810 (± 627) at Station 1 (maximum), whereas the total number of species per station varied from 16 (at Station 7) to 33 (at Station 4).

Table 1. Characteristics of vegetation and bottom of the *Zostera* Stations near Roscoff.

Station number		1	2	3	4	5	6	7
Height in littoral[1]	MHWN	———			———			———
	MLWN		———	———		———		
	MLWS						———	
Sediment structure (dry weight percentages)								
Sediment	Equivalent diameter (μm)							
coarse sand	> 200	0	1.9	3.0	46.5	61.8	80.0	60.2
fine sand	50–200	9.8	70.2	65.1	37.4	37.7	18.0	39.4
coarse silt	25–50	49.9	21.0	24.4	3.6	0.2	1.4	0.3
fine silt	2–25	35.6	5.8	6.5	12.2	0.1	0.4	0
clay	< 2	4.8	1.1	1.0	0.3	0.1	0.2	0
Dry organic content		9.6	2.5	3.2	2.9	1.5	1.0	0.8
Vegetation								
Zostera marina:								
mean number of shoots m^{-2}				2730	590	1130	270	
SE (%)				8.1	10.2	6.2	11.1	
mean length of shoots (cm)				22.7	28.8	8.7	18.9	
Zostera noltii:								
mean number of shoots m^{-2}		15600	4110					5320
SE (%)		9.0	12.7					12.8
mean length of shoots (cm)		7.7	12.9					7.0
Epiphytic algae[2]		–	+	–	+	+	+ +	+
Mat of algae[2]		–	–	–	+ +	–	–	–

[1] H = high; M = mean; L = low; HW = high water; LW = low water; S = spring tide; N = neap tide.

[2] – absent; + few; + + abundant.

The differences between the assemblages at the stations are illustrated by the diversity indices calculated for the total benthic fauna (Table 4). Hence, the assemblages with the highest diversity with respect to the distribution of individuals among the species were found at the Stations 3 and 6 (both *Zostera marina* stands). Station 7 (the *Z. noltii* bed near Penpoul) showed the lowest species diversity, indicating a rather simple habitat structure. Particularly in

Table 2 Numbers of epifaunal species (totals of 6 subsamples) of different *Zostera* Stations near Roscoff.

Station number	1	2	3	4	5	6	7
Species							
Jaera forsmani Bocquet (I)	4						
Akera bullata Müller (G)	1						
Hydrobia ulvae (Pennant) (G)	208	6					2
Littorina littorea (Linnaeus) (G)	13	8	4				
Idotea chelipes (Pallas) (I)	3	2	2				
Carcinus maenas (Linnaeus) juv (D)	3	2	2	1	1	1	1
Edwardsia sp (An)	2						
Halcampa chrysanthellum (Peach) (An)			2		1		
Cereus pedunculatus (Pennant) (An)			1				
Anemonia sulcata (Pennant) (An)			2				
Molgulidae sp. (T)			4				
Rissoa membranacea (Adams) (G)			1				
Palaemon serratus (Pennant) (D)			8				
Gammarus c f *locusta* (Linnaeus) juv. (A)		1	17			8	2
Bittium reticulatum (Da Costa) (G)		1	1	1			
Amphipholis squamata (Delle Chiaje) (E)			3	50			
Gibbula pennanti (Philippi) (G)			1	5			
Gibbula umbilicalis (Da Costa) (G)				5			
Cingula semicostata (Montagu) (G)				30			
Rissoa guerini Recluz (G)				2			
Rissoa parva (Da Costa) (G)				3			
Ocinebrina aciculata (Lamarck) (G)				1			
Ocenebra erinacea (Linnaeus) (G)				1			
Pomatoschistus pictus (Malm) (Pi)				1			
Pagurus bernhardus (Linnaeus) (D)				1			
Stenothoe monoculoides (Montagu) (A)				1			
Pherusa fucicola Leach (A)				3			
Microprotopus longimanus Chevreux (A)				2			
Janira maculosa Leach (I)				1			
Iphinoe tenella Sars (C)				4		4	
Anoplodactylus angulatus (Dohrn) (P)			1			2	
Dexamine thea Boeck (A)				1		2	
Aora gracilis Kröyer (A)						1	
Perioculodes longimanus (Bate and Westwood) (A)						1	
Leucothoe incisa D Robertson (A)						1	
Macropodia rostrata (Linnaeus) (D)						1	
Odostomia sp (G)						1	
Corophium sp (A)							1

A = Amphipoda, An = Anthozoa, C = Cumacea, D = Decapoda, E = Echinodermata, G = Gastropoda, I = Isopoda, P = Pycnogonida, Pi = Pisces, T = Tunicata

Table 3. Numbers of infaunal species (totals of 6 subsamples) of different *Zostera* Stations near Roscoff

Station number	1	2	3	4	5	6	7
Species							
Streblospio shrubsolii (Buchanan) (PS)	1						
Scrobicularia plana (Da Costa) (B)	2	1					
Tharyx marioni (Saint-Joseph) (PS)	152	45				3	
Abra c.f. *alba* (Wood) (B)	23	3		1			
Fabricia sabella Ehrenberg (PS)	22	2	2				
Ampharete acutifrons (Grube) (PS)	34	109	8				
Lineus c.f. *viridis* (Fabr) Johnston (N)	3	6					
Mellina palmata Grube (PS)	1	13					
Prionospio malmgreni Claparède (PS)		1					
Eteone longa (Fabricius) (PE)		2					
Polydora caeca (Oersted) (PS)		29					
Malacoceros fuliginosus (Claparède) (PS)	1	1			2		
Heteromastus filiformis (Claparede) (PS)	7	5	4		3	2	
Lanice conchilega (Pallas) (PS)			2				
Mysella bidentata (Montagu) (B)			4				
Nephtys hombergi Savigny (PE)			1				
Eumida sanguinea Oersted (PE)			1				
Glycera alba (Müller) (PE)		1	1		1		
Parvicardium exiguum (Gmelin) (B)			1	1			
Syllidae spp. (PE)	1	1		8			
Harmothoe lunulata (Delle Chiaje) (PE)			3			1	
Cerastoderma edule (Linnaeus) (B)	3						2
Pygospio elegans Claparède (PS)	227	71	2			3	236
Anaitides mucosa (Oersted) (PE)		4			4	1	3
Platynereis dumerilii (Audouin & Milne-Edwards) (PE)			5	28	6	4	
Notomastus latericeus Sars (PS)		7	4	16	20	4	4
Sabella penicillus Linnaeus (PS)			1	1		1	
Arenicola marina (Linnaeus) (PS)				1			
Megalomma linaresi (Rioja) (PS)				1			
Lucinoma borealis (Linnaeus) (B)				3			
Apseudes latreillei (Milne-Edwards) (T)				209	1		
Aonides oxycephala (Sars) (PS)				11	4		
Lumbrineris latreilli Audouin & Milne-Edwards (PE)				7	4		
Amphitritides gracilis (Grube) (PS)				1	1		
Syllidia armata Quatrefages (PE)			1			2	
Polydora flava Claparède (PS)			1		10		
Capitella capitata (Fabricius) (PS)	1	1	1			3	1
Nereis caudata Delle Chiaje (PE)					1		
Euclymene c.f *oerstedi* (Claparède) (PS)				4	41	22	
Loripes lacteus (Linnaeus) (B)				1	46	10	2
Spio filicornis (Müller) (PS)					8	2	1
Polycirrus aurantiacus Grube (PS)						1	
Scoloplos armiger (Müller) (PS)		1			5	4	9
Leiochone clypeata Saint-Joseph (PS)						3	3
Urothoe grimaldii Chevreux (A)						4	4
Marphysa bellii (Audouin & Milne-Edwards) (PE)						1	1
Caulleriella bioculatus (Keferstein) (PS)							1

A = Amphipoda, B = Bivalvia, N = Nemertini, PE = Polychaeta Errantia, PS = Polychaeta Sedentaria; T = Tanaidacea

comparison with the other *Z. noltii* Stations, the low species diversity at Station 7 was peculiar. *Pygospio elegans* was the only numerically dominant species (see Tables 2 and 3) at that Station and was responsible for the low diversity values. The Stations 1, 2, 4 and 5 showed intermediate diversity values and were characterized by either no or more dominants (see Tables 2 and 3). Comparison of this pattern in diversity values with the depth distribution of the concerning *Zostera* stands (Table 1) showed a remarkable result: an increasing tidal depth or an increasing water coverage correlated with a higher diversity of the faunal assemblage. Station 4 was the exception to this rule; there the diversity was rather low with respect to the depth, due to the occurrence of one single dominant species, i.e. *Apseudes latreillei.*

An assessment of the percentage similarity was made by comparing all pairs of Stations (Fig. 2). The resulting percentages appeared to be very low, as a consequence of a great variability in species composition (see Tables 2 and 3). The Stations with a *Zostera noltii* community (Stations 1, 2 and 7) are mutually more similar than the *Z. marina* communities. Other groups of Stations with a considerable affinity to each other were 6 & 3, and 6 & 5. The percentage similarity data in Fig. 2 showed no relation to the tidal position of the Stations, as described above for the diversity values. In addition, comparison with the sediment composition provided no evidence of a direct correlation: in that case the pairs of Stations with subsequent ranking numbers (e.g. 1 and 2, 2 and 3, etc.) should show the highest similarity, i.e. diagonally from up-left to down-right in Fig. 2. Since the possible effects of sediment properties upon faunal

Table 4. Faunal characteristics of the *Zostera* Stations near Roscoff (N = number of individuals; S = number of species; SE = standard error; H = Shannon index; J = evenness, d = Margalef index).

Station number	1	2	3	4	5	6	7
Seagrass	*Zostera noltii*	*Zostera noltii*	*Zostera marina*	*Zostera marina*	*Zostera marina*	*Zostera marina*	*Zostera noltii*
Fauna (epifauna + infauna)							
Total S	21	25	31	33	18	28	16
Total N m^{-2}	18810	8462	2384	10637	4166	2436	7152
SE	627	1592	279	1449	492	378	2021
Diversity H	1.78	2 09	3 04	1.95	2 13	2.85	0 73
Diversity J	0 58	0 65	0.89	0.56	0 74	0.86	0 26
Diversity d	3.04	4.15	6.65	5 33	3.35	5.97	2.67
Benthic infauna							
Total S	14	19	17	15	16	18	12
Total N m^{-2}	12680	7938	1100	7676	4113	1860	6995
SE	453	1537	190	1018	481	291	2045
$N_{infauna}/N_{infauna + epifauna}$ (%)	67	94	46	72	99	76	98
Diversity H	1 45	1 88	2 58	1.18	2 07	2 42	0.61
Diversity J	0.55	0.64	0 91	0 43	0 75	0.84	0.24
Diversity d	2.10	3 15	4.28	2.46	2 97	3 99	1 97

composition can be assumed to concern mainly the animals strictly bound to the substratum, the epifauna (see Table 2) was excluded. However, as for some animals the exact determination of the habitat was very difficult to define, such a segregation of epifauna and benthic infauna seemed disputable for a number of species. For the benthic infauna given in Table 3 (on the average 79% of the total number of individuals, see Table 4) the percentage similarity for all pairs of Stations was calculated. After classification sorting analysis, the results were schematized in a dendrogram (Fig. 3). Two separate groups could be distinguished: Stations 1, 2 and 7 (the *Zostera noltii* communities) and Stations 5 and 6. These groups showed a similarity exceeding 40%. The Stations 3 and 4 had a very low similarity with the other ones. The Station numbers in Fig. 3 do not appear to be arranged according to their numerical sequence, i.e. according to an increasing sand fraction and a decreasing fraction of silt and clay. It can be concluded, therefore, that in general there was no direct relation between the sediment properties and the composition of the faunal assemblages of the described seagrass stands.

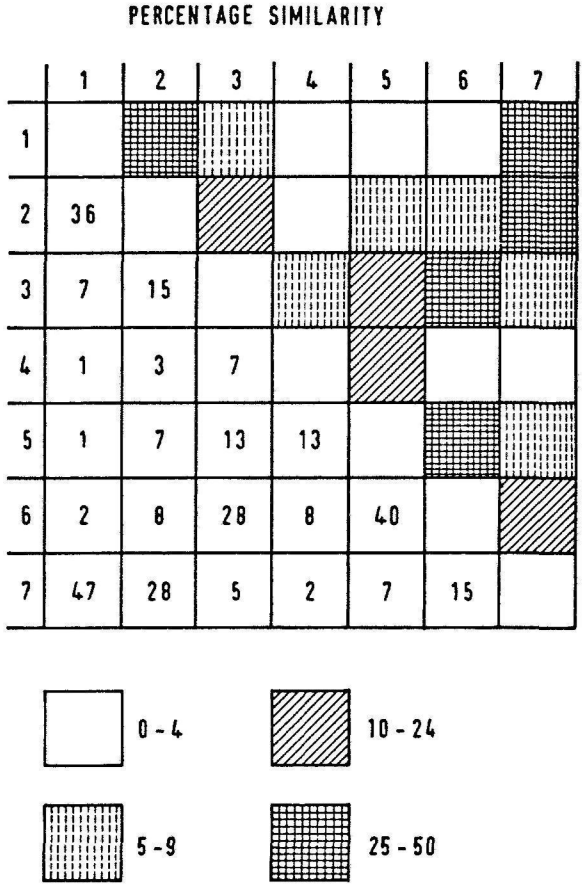

Fig. 2. Comparison of the percentage similarity of the benthic macrofauna between pairs of *Zostera* Stations near Roscoff.

In order to achieve a synthesis of factors determining the species composition of the faunal assemblages, species were arranged in such a way that the differences between the Stations were easily recognizable (see Tables 2 and 3). These differences were analysed and related to the characteristics of the different seagrass stands, as given in Table 1.

Roughly the infauna can be divided into three groups (see Table 3):

1. species occurring mainly in silt bottoms, i.e. the first 13 species of the *Zostera noltii* communities near Locquénolé and Tenerez (Stations 1 and 2);
2. species occurring mainly in sand bottoms, i.e. the last 10 species in Table 3;
3. the remaining group seems to be more or less indifferent and independent of the sediment composition. However, some of the species seem to be characteristic for a distinct sediment structure.

The high affinity between the total faunal assemblages of the *Z. noltii* communities situated on the tidal mud flats near Locquénolé (Station 1) and near Tenerez (Station 2) was mainly caused by species which seem to be characteristic for such communities high in the littoral (c.f. Moore, 1964;

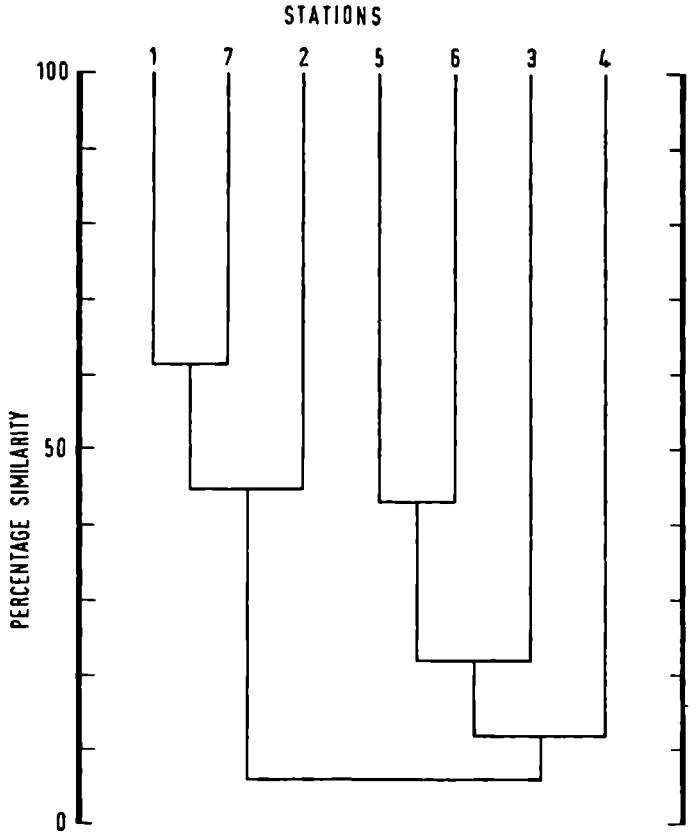

Fig. 3. Dendrogram of benthic infaunal affinities between different *Zostera* Stations near Roscoff.

Wolff, 1973; Nelson-Smith, 1977). The resemblance to a *Z. noltii* community in the German Wadden Sea is remarkable. Here Reise (1978) found the following species to be most abundant: *Hydrobia ulvae*, *Fabricia sabella*, *Pygospio elegans*, *Capitella capitata*, *Arenicola marina* (juv.), *Scoloplos armiger*, *Polydora ligni* Webster and *Malacoceros fuliginosus*. The Stations 1 and 2 were situated in areas where tidal currents were of lesser importance, so that finer particles could sink to the bottom. This material was caught between the seagrass leaves and was responsible for the high organic content and the muddy structure of the bottom (see Table 1). These muddy locations were inhabited by a dense infaunal assemblage of deposit-feeding tube-building polychaetes, of which the overwhelming dominants of Stations 1, i.e. *Tharyx marioni* and *Pygospio elegans* (see Table 3), showed an extraordinary high abundance of 9930 ind. m^{-2} (SE = 877). The density of the *Zostera noltii* vegetation also affected the composition of the epifauna (Table 2). The snails crawling on the leaves were more numerous in the dense bed, i.e. Station 1 near Locquénolé (see Table 1). The mudsnail, *Hydrobia ulvae*, showed the highest density at Station 1: 5450 ind. m^{-2} (SE = 300) on average. The absence of epiphytic algae on the leaves was coupled with high numbers of these gastropods. The very low number of gastropods at Station 2 near Tenerez concurred with the presence of epiphytic algae (mainly diatoms).

The high resemblance of Stations 1 and 2 to Station 7 was mainly based on the high numbers of *Pygospio elegans* (Table 3), occurring at Station 7 with mean numbers of 6200 ind. m^{-2} (SE = 2300). Although the habitat structure of Station 7 (*Zostera noltii* near Penpoul) resembled that of Stations 1 and 2, the coarse-grained sediment with a very low organic content (see Table 1) was inhabited by a different faunal assemblage with a lower number of species and a low diversity (see Table 4). Nevertheless, two samples of 64 cm^2 each, taken just outside the *Z. noltii* bed, showed an even more sparsely populated sand bottom. These samples contained only the polychaetes *Marphysa bellii* (1 ind.), *Spio filicornis* (1 ind.), *Pygospio elegans* (5 ind.) and *Leiochone clypeata* (1 ind.) and 2 individuals of the burrowing amphipod *Bathyporeia pilosa* Lindstrøm.

The H-values of the faunal assemblages of the four *Zostera marina* communities were higher than those of the *Z. noltii* communities at Stations 3, 5 and 6, but lower at Station 4 (see Table 4). The last comparatively low diversity value was due to the numerical abundance of four species. The presence of epiphytic algae and mat of algae between the eelgrass shoots at Station 4 (see Table 1) formed a variety of micro-habitats, each with a specific dominant(s). The complexity of this community was apparent by the presence of several smaller crustacean and gastropod species (Tables 2 and 3), resulting in the highest total S of all Stations. The dominant epifaunal species were the ophiuroid *Amphipholis squamata* (1310 ind. m^{-2}; SE = 260) and the gastropod *Cingula semicostata* (790 ind. m^{-2}; SE = 380). The particular habitat formed by the thick rhizome mat was characterized by the tanaidacean *Apseudes latreillei* (5480 ind. m^{-2}; SE = 770) and the polychaete *Platynereis dumerilii* (730 ind. m^{-2}; SE = 170). These last two species were found in the top layer of the bottom.

Station 3 (the *Zostera marina* community near Tenerez) was located in a very dense eelgrass bed situated in a tidal pool (see Table 1). The fauna of this habitat was characterized by a high diversity, without overwhelming dominants. This diversity and also the presence of sea-anemones, ascidians and decapods indicated a community structure which was complex but fairly stable because of the relatively narrow range of features of the abiotic environment. Although Station 3 was situated close to Station 2 and the sediment structure of both Stations was comparable (Table 1), the difference between their infaunal assemblages was remarkable (see Table 3). The sublittoral character of Station 3 (i.e. the tidal pool) probably led to a lack of dominant deposit feeding polychaetes characteristic for the upper littoral flats and subsequent replacement by several species of errant polychaetes.

The infauna of the Stations 5 and 6 showed a considerable similarity, i.e. 43% (see Fig. 3), corresponding to a similar sediment structure. Differences in the values for H (Table 4) were only caused by the presence of more species with a relatively high abundance at Station 5, i.e. *Notomastus latericeus* and *Polydora flava*. However, in a comparison of the total assemblages, the similarity was only 40%, due to a rich fauna of smaller crustaceans (mainly amphipods) at Station 6 and a near absence of other epifaunal species at both Stations (see Table 2). The amphipods at Station 6 were strictly associated with enormous quantities of epiphytic algae, mainly Ectocarpaceae and tube-forming Bacillariophyceae, on the eelgrass leaves. Thorough examination of 25 eelgrass shoots by immersion in 4% formalin, according to a method described by Truchot (1963), provided the following species: *Gammarus locusta* (24 ind.), *Dexamine spinosa* (Montagu) (1 ind.), *Aora gracilis* (7 ind.), *Amphithoe gammaroides* Bate (7 ind.) and *Ericthonius brasiliensis* (Dana) (2 ind.).

SPATIAL DISTRIBUTION

The arithmethic means of all combinations of subsamples using an increasing sample size were calculated and the species-area relationship was determined for each Station. For each discrete assemblage there was a specific relationship between species number and the size of the sampled area (Table 5). None of the Stations showed a specific minimum area which included all species. However,

Table 5. Relation between the mean numbers of species (S) and the sampling area (in cm^2) of different *Zostera* beds near Roscoff.

Station number	Regression equation
1	$S = 12.14 \log x + 38.29$
2	$S = 18.24 \log x + 50.41$
3	$S = 27.56 \log x + 69.36$
4	$S = 26.01 \log x + 68.72$
5	$S = 12.24 \log x + 35.34$
6	$S = 23.48 \log x + 60.64$
7	$S = 14.06 \log x + 35.54$

estimation by regression equations showed that a doubling of the total sampling area provided only a slight increase in the total number of species: in the 6 subsamples 79–85% of all species were found, calculated for 12 subsamples. In addition, these percentages were maximum values, for it was possible that the faunal assemblage at a particular Station had a minimum area smaller than 12 subsamples (this would occur in communities with low species capacity, i.e. communities with a poorly diversified structure).

The distribution pattern of the individuals within the assemblages is influenced by the size of the subsamples (Rosenberg, 1977; Elliott, 1977). Increasing sample size may change a contagious distribution into firstly a random, then a contagious and finally a regular distribution. Other factors determining the spatial pattern are the structure of the habitat, intra- and interspecific relations, etc. Because of the great differences in numbers of species present in the samples taken from the seagrass beds, it seemed incorrect to calculate the spatial distribution separately on the basis of only 6 subsamples. Therefore the actual dispersion analysis was only executed for the whole assemblages on the basis of 6 subsamples of 0.038 m^2 each. The results showed a contagious distribution of the fauna at the Stations 2, 4, 6 and 7 and a random distribution at the Stations 1, 3 and 5. The occurrence of a contagious distribution at the Stations 2, 4, 6 and 7 was not surprising, for the most important structural element, i.e. the seagrass itself, was distributed unevenly. This was apparent by the more or less patchy structure of the beds, shown by the mean numbers of shoots m^{-2} with the highest deviations at those Stations (see Table 1). Conversely, Stations with a rather homogeneous habitat structure showed a random distribution of individuals.

Some knowledge of the niches of the most abundant species (see Table 6) would help in understanding the community structure and the distribution of the species. The majority of the animals in the benthic assemblages were of the same trophic group – detritivores. The sampling method used was inadequate for carnivores, although some species were found. However, only juveniles of larger predatory species (e.g. epifaunal invertebrates and fish) were sampled. Evaluating the feeding type of the infaunal dominants at all Stations, the importance of sediment type was illustrated by a shift from selective deposit feeders to non-selective deposit feeders from Station 1 to Station 7. This concurred with an increase in the sand fraction of the sediments. The non-selective deposit feeders were usually only the maldanid and capitellid polychaetes, which are positioned vertically in the bottom with their anterior ends in the sediment. They influence the sediment structure by ingesting only the fine-grained particles and by transporting these to the bottom surface (Rhoads, 1974). The seagrass beds at the Stations 1, 2, 5 and 7, which were situated high in the littoral, could be defined as communities in which most species live on comparatively few basic sources of food, i.e. simply structured communities. The most abundant species were benthic deposit and suspension feeders, obtaining their food from detritus either in or on the sediment. The high density of small animals at the muddy Stations 1 and 2 was remarkable,

but agrees with data from Stanley (1970), who stated that there is a general tendency for species to be small as the percentage mud increases to over 25%.

The Stations 3, 4 and 6 were situated lower in the littoral or else showed sublittoral tidal pool characteristics (as Station 3). These contained communities in which species live on several sources of food, i.e. more complexly structured communities (see Table 6 for the dominant species). The

Table 6. Ranking order of the five most abundant species and their feeding type at the distinguished *Zostera* Stations. The highest possible score (biological index) per species amounts to 33.3%.

Station number	Most abundant species	Biological index (%)	Feeding type[1]
1	*Pygospio elegans*	30.0	SDF
	Hydrobia ulvae	27.8	SDF
	Tharyx marioni	22.2	SDF
	Ampharete acutifrons	7.8	SDF
	Abra c.f. *alba*	4.4	SF
2	*Ampharete acutifrons*	33.3	SDF
	Pygospio elegans	22.2	SDF
	Tharyx marioni	17.8	SDF
	Polydora caeca	13.3	SDF
	Littorina littorea	6.7	O
3	*Gammarus* c.f. *locusta*	21.1	DF-H
	Ampharete acutifrons	16.7	SDF
	Palaemon serratus	12.2	O
	Platynereis dumerilii	10.0	H
	Littorina littorea	7.8	O
4	*Apseudes latreillei*	33.3	S
	Amphipholis squamata	24.4	DF-S
	Platynereis dumerilii	15.6	? H
	Cingula semicostata	13.3	SDF
	Notomastus latericeus	5.6	NSD
5	*Loripes lacteus*	30.0	SF
	Euclymene c.f. *oerstedi*	27.8	NDF
	Notomastus latericeus	17.8	NDF
	Spio filicornis	7.8	SDF
	Polydora flava	6.7	SDF
6	*Euclymene* c.f. *oerstedi*	31.1	NDF
	Loripes lacteus	21.1	SF
	Gammarus c.f. *locusta*	13.3	DF-H
	Notomastus latericeus	5.6	NDF
	Urothoe grimaldi	5.6	? SF
7	*Pygospio elegans*	32.2	SDF
	Scoloplos armiger	18.9	NDF
	Notomastus latericeus	8.9	NDF
	Leiochone clypeata	6.7	NDF
	Anaitides mucosa	5.6	S

[1]SDF = selective deposit feeder; NDF = non-selective deposit feeder; SF = suspension feeder; S = scavenger; H = herbivore; O = omnivore.

increased habitat complexity caused a greater abundance of above-ground mobile animals, for which the relatively long eelgrass leaves (see Table 1) also provided a refuge. Comparison with the data from Ledoyer (1962, 1964a, 1964b) illustrates that the sampling method applied was insufficient for the exact determination of the numbers of these mobile species.

DISCUSSION AND CONCLUSIONS

From a consideration of the relationships between abiotic factors and species diversity, stability of the environment has been proposed as leading to complex structured communities (Sanders, 1968, 1969). Variations in structural complexity may well be produced by environmental dynamics, e.g. salinity, water depth and daily temperature fluctuations. Salinity is an important factor affecting the distribution and diversity of any aquatic fauna (Gunter, 1961; Boesch, 1972; Wolff et al., 1977; Verhoeven, 1980). In the Roscoff area salinity of ocean water is nearly constant throughout the year and water temperature changes very slowly with minimum values of approximately 9°C in February – March and maximum values of approximately 15°C in August – September (Anonymous, 1976). However, temporal variability in water coverage in the littoral area (i.e. high water and low water) may cause large fluctuations in salinity and temperature. These influences on the seagrass beds are most pronounced at low water spring tide, which always occurs at midday at Roscoff. In addition, Station 1 is situated high in the estuary and during high tide this *Zostera* bed is in contact with sub-oceanic salinities. Any temporarily unfavourable factor eliminates certain species and creates habitats for opportunistic species with suitable morphological and physiological adaptations. In this study such habitats were found in the muddy Stations high in the littoral. In general, mud bottoms show a less diverse fauna than sand bottoms, presumably because of the smaller variety of micro-habitats (Sanders, 1968). But since in the vicinity of Roscoff mud bottoms are usually situated higher in the littoral than sand bottoms, one must be cautious in attributing differences in faunal assemblages to sediment structure and other physical factors. As physical stability increases with increasing water depth, a depth gradient is characterized by increasing diversity. This was also noted by Sanders (1969) and Day et al. (1971) for the deep sea and by Johnson (1970) for the littoral belt. However, diversity describes the organization of the community in terms of species richness and species abundance, but is independent of species identity. Changing species-selection is an implicit factor in changing micro-habitats along the depth-related gradient, resulting in a simultaneously changing composition of the faunal assemblage. This fact is accentuated by an increasing complexity of the floristic elements of the seagrass community with increasing depth. Due to the rather stable character of most seagrass beds themselves (Blois et al., 1961; Den Hartog, 1973; Jacobs, 1979a) and the fact that the seagrasses are productive all year round (Jacobs, 1979a; Jacobs & Noten, 1980), the communities near Roscoff may be considered to be structurally stable. This may imply that each separate bed internally maintains

an approximately steady state, i.e. a biocoenotic homeostasis. Thus the differences between the beds were caused by differences in the abiotic environment, and, taking into account the pattern in diversity values, this implies an increasing environmental stability with increasing water coverage.

Diversity in the seagrass beds, measured by the rarefaction method (Sanders, 1968), allows direct comparison of samples with differing numbers of individuals. This may be taken to represent a summary of the results (see Fig. 4), the more so as in this case the results concern samples of comparable size. Communities of physically unstable habitats are characterized by the smallest numbers of species: habitats with a reduced water coverage comply with these conditions most closely, i.e. Stations 1 and 7. The other end of the diversity spectrum includes habitats with fairly constant physical conditions and a complex structure. Comparison of the total numbers of N and S in Fig. 4 and their ratio, may show the presence of one or more dominant species, e.g. at Station 1. In addition, this spectrum indicates the complexity of the vegetation structure with as most important elements: the rhizome layer, the mat of algae between the seagrass shoots, the seagrass shoots and the epiphytic algae on the leaves. The structure of the community has great influence on the fauna inhabiting the plant beds: Stations with more niches available for the fauna show a low N/S ratio. These are the more physically stable habitats.

A number of investigations have been made into the fauna of *Zostera marina* communities (Orth, 1973; Marsh, 1973; Lappalainen & Kangas, 1975; Thayer et al., 1975). All these studies concerned eelgrass beds under permanently submerged conditions. Comparison of these communities is only possible by taking advantage of diversity values, as these are independent of the species composition. The H values for the eelgrass community near Tvärminne, Finland (Lappalainen & Kangas, 1975), ranging from 0.78–2.13 seem to be rather low, probably due to more brackish conditions (see Verhoeven, 1980) in that area. Thayer et al. (1975) studied an eelgrass community in Newport River estuary (North Carolina); they gave H values for epifauna and infauna separately. The indices for the infauna ranged from 1.2–1.5 and for the epifauna from 0.6–1.4. They imputed the low diversity to the young and evolving status of the community, because in a more mature bed of the York River (Virginia) Marsh (1973) found indices of 1.92–3.90 for the epifauna. The H values for the Roscoff area show the same range as those described above. However, taking into account the sublittoral character of all these communities, the indices for the most complex (littoral) communities near Roscoff are relatively high (up to 3.04). Only Orth (1973) and Marsh (1973) gave higher values (up to 4.05 and 3.90 respectively), probably caused by a rich amphipod fauna, the abundance and diversity of which in *Zostera* communities may be very high (see also Toulmond & Truchot, 1964; Nelson, 1979; Caine, 1979). During this investigation in the Roscoff area we only found a few amphipod species. This is an artifact due to the Amoco Cadiz oil spill of March 1978, for the amphipod fauna was much richer before this spill (Jacobs, 1979b, 1980; Den Hartog & Jacobs, 1980). Data concerning the situation before the

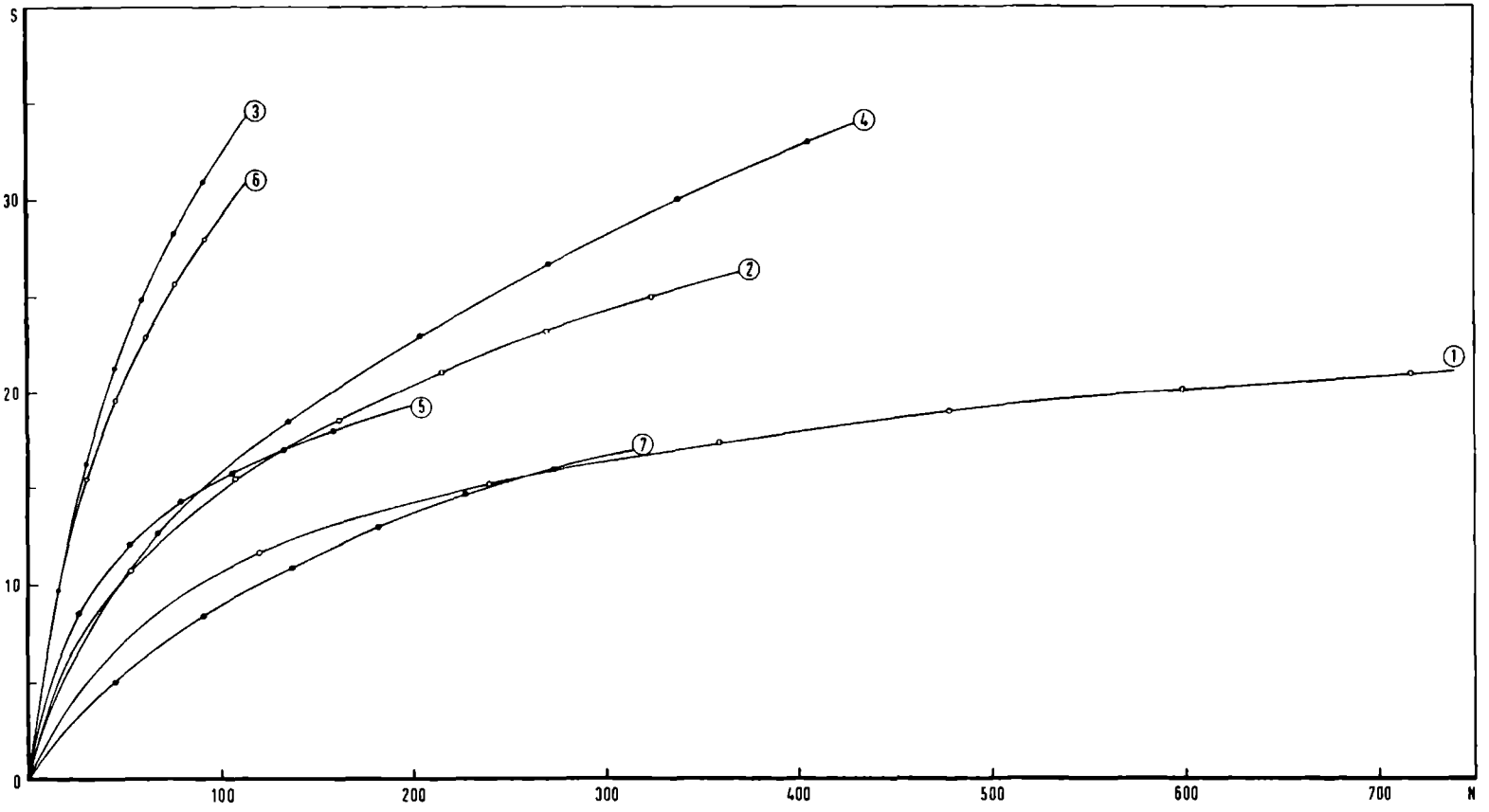

Fig. 4. Rarefacted diversity curves for the benthic macrofauna of different *Zostera* Stations in the vicinity of Roscoff (N = number of individuals; S = number of species).

impact are only available for the Stations 3 and 4, and therefore only these Stations loan themselves to comparison. The more complex community at Station 4 showed a particularly rich amphipod fauna before the spill (Jacobs, 1980; Den Hartog & Jacobs, 1980). The virtual absence of the Amphipoda caused a decrease of the H values from approximately 2.5 before the spill (the beginning of 1978) to approximately 2.0 in May 1979.

The macrofauna composition in the *Zostera* habitats shows such differences that a general classification of the communities with respect to their fauna composition seems to be useful and necessary. For this purpose the phytosociological classification of *Zostera* communities based on floristic, structural and dynamic characteristics of the seagrass vegetation (Den Hartog, 1976, 1977) seems too inexact, even though the structure of the macrophyte community appears simple and uniform. However, the zosterids show great differences in growth form with small-leaved and long-leaved shoots as phenological extremes. In addition, the morphological diversity of the *Zostera* shoots is shown by several transitional cases between the extremes. Jacobs (1979a) found that the growth form can give an indication of environmental conditions, particularly water coverage, for which a direct relation exists with the length of leaves and the number of shoots m^{-2}. This abiotic factor thus causes a zonation pattern in the monospecific *Zostera* beds. A vertical pattern in the vegetation is related to the horizontal pattern described, for communities of long-leaved zosterids are characterized by several vegetation layers. It appears from this investigation that these layers consist of micro-habitats of algae, in addition to the vertically separated *Zostera* layers (e.g. leaves, leaf sheaths, rhizomes). The number of these micro-habitats decreases towards the communities of small-leaved forms. All these micro-habitats are characterized by their own specific faunal assemblages. In order to come to a natural system comprising the total biocoenoses, as indicated by Den Hartog (1977, 1979) and recently applied by Verhoeven (1980) in an attempt to classify *Ruppia*-dominated communities in Western Europe, the faunal assemblages should be incorporated. Generalization is hampered through differences in species composition, caused by differences in geographical latitude and salinity, though these are independent of vegetation structure. It is proposed that the *Zostera* biocoenoses be distinguished according to criteria which indicate the number and characteristics of the micro-habitats. From this investigation it follows that qualification of the biocoenoses, including the faunal assemblages, is possible by regarding the following structural characteristics:

1. the life-span of the *Zostera* bed, i.e. annual or perennial vegetations;
2. habitat characteristics of the bed related with the percentage water coverage, i.e. plants growing under eulittoral conditions or permanently submerged. Both cases occur with annual as well as perennial beds;
3. structural characteristics of the macrophyte vegetation, i.e. the number of shoots m^{-2}, the length of the shoots and the thickness of the rhizome mat;
4. structural characteristics of the epiphytic vegetation: only encrusting diatoms or a more luxurious vegetation of Chlorophyta, Phaeophyta and Rhodophyta or tube-forming diatoms;

5. presence of a mat of algae between the seagrass shoots;
6. bottom characteristics, i.e. a sandy or muddy bottom structure.

The two first mentioned characteristics also determine the manifestation of the characteristics 3, 4 and 5 and in some extent 6, and hence the faunal assemblages.

In an attempt to classify the *Zostera* biocoenoses near Roscoff, the authors propose the following units:

1. Biocoenoses of *Zostera noltii* stands under eulittoral conditions on muddy bottoms (Stations 1 and 2). Simply structured communities with a dense benthic fauna, of which the majority belong to the selective deposit feeders.
2. Biocoenoses of *Zostera noltii* stands under eulittoral conditions on sandy bottoms (Station 7). Simply structured communities with a dense benthic fauna, of which the majority belong to the non-selective deposit feeders.
3. Biocoenoses of perennial *Zostera marina* stands under both eulittoral and submerged conditions, forming a continuum with numerous intermediate forms. Sub-biocoenoses can be distinguished by qualification and quantification of the structural elements in the vegetation (Stations 3, 4, 5 and 6).

This classification, based on floristic, structural and ecological criteria, seems to be the best available at present. This was also indicated by Den Hartog (1979). Faunistic criteria at species level appear useless and unnecessary for the purpose of classification, as richness and diversity of the fauna are directly correlated with the structure of the vegetation. The faunistic criteria can be applied to subdivide the biocoenoses at local level.

The authors realize that this approach is only a first attempt to classify the *Zostera* biocoenoses near Roscoff and a more general classification requires more data from different habitats.

ACKNOWLEDGEMENTS

We would like to thank Professor Dr. C. den Hartog, Dr. L. Cabioch and Dr. J.T.A. Verhoeven for critically reviewing the manuscript and Connie A.N. van Oorschot for correcting the English text. We are also indebted to Dr. J.C. den Hartog (Leiden) for the identification of some sea-anemones, Dr. G. Hartmann-Schröder (Hamburg) for her identification of *Megalomma linaresi*, Mr. J.G.M. Roelofs for assistance with the bottom analysis and Mr. J.J.A. Slippens for the drawings. We thank Professor Dr. J. Bergerard and his staff, who provided accomodation at the Station Biologique at Roscoff. This investigation was financially supported by the "Naples-Roscoff Commission" of the "Nederlandse Akademie van Wetenschappen".

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SEASONAL VARIATIONS IN THE STRUCTURE OF A ZOSTERA COMMUNITY ON TIDAL FLATS IN THE SW NETHERLANDS, WITH SPECIAL REFERENCE TO THE BENTHIC FAUNA

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ABSTRACT

The ecology of a seagrass community, dominated by Zostera noltii Hornem. and the annual form of Z. marina L. was studied intensively during an entire year. The meadow was situated on the tidal flats in the Krabbenkreek, a blind arm of the Oosterschelde in the SW Netherlands. The structure and dynamics of the macroflora and macrofauna were examined at two different levels in the littoral. The sampling stations were characterized by differences in abundance of the two seagrass species, detailed information was presented concerning species distribution, seasonal fluctuations in cover and above- and below-ground biomass. Temporal patterns in the vegetation were strongly affected as a result of plant species adaptation to the environment, manifested in characteristic life-strategies. During the winter the vegetation was heavily grazed by waterfowl.

The macrofauna inhabiting the Zostera bed was examined by studying the patterns of species occurrence and abundance. A total of 35 taxa were found during the investigation period. The fauna in the high littoral bed, dominated by Z. noltii, showed the following characteristics: on the average 18,000 individuals m^{-2}; the diversity index H_2 ranged from 1.22 to 1.98; an average biomass of 111.4 g dry wt m^{-2} and 14.8 g ash-free dry wt m^{-2}. For the lower bed, temporarily dominated by Z. marina, these characteristics were: 22,500 ind.m^{-2}; H_2 ranged from 1.07 to 1.80; an average biomass of 181.7 g dry wt m^{-2} and 20.1 g ash-free dry wt m^{-2}. The differences in species composition and abundance between the two beds were not directly related to the plant species, but more to differences due to the height in the littoral. Within the faunal assemblage three major groups were distinguished: (1) species with a strong numerical dominance, characteristic for the tidal flats high in

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the littoral, (2) species more or less structurally related to the seagrass vegetation, (3) incidental inhabitants.

It was concluded that the structure of the community was organized simply and characterized by the following features: temporary presence of vegetation, low diversity in the frame-elements of the plant community, numerical dominance of non-selective deposit-feeding animal species, no direct trophic relation between fauna and seagrass. In addition, in terms of ash-free dry weight, the dominant animal species were represented in all trophic levels and apparently occupied all available niches.

INTRODUCTION

Zostera species in the northern Atlantic are not only restricted to subtidal marine environments, but can also be found under tidal conditions (Den Hartog, 1970; Bayer, 1979; Harrison, 1979; Jacobs, 1979; Denis, 1980; Jacobs and Huisman, 1982), and in brackish waters (Luther, 1951a, 1951b; Van den Hoek, 1968; Nienhuis and De Bree, 1977; Verhoeven and Van Vierssen, 1978; Verhoeven, 1980). In the subtidal areas, which are physically and biologically relatively undisturbed, Zostera marina L. (eelgrass) forms perennial populations characterized by an asexual vegetative expansion of the rhizomes (see discussion by Jacobs, 1982). In temperate intertidal habitats, the plants are subjected to tidal and/or annual fluctuations of environmental factors. As a consequence, some of the populations at the intertidal level consist of annual plants, which establish each year from seeds (Keddy and Patriquin, 1978; Bayer, 1979; Denis, 1980). These populations are often mixed with populations of Zostera noltii Hornem. in Europe (Denis, 1980; Jacobs and Huisman, 1982), or Z. americana den Hartog in Pacific Canada (Harrison, 1979).

In recent years several authors have described aspects of the identity, the distribution and the life-history patterns of the annual and perennial Z. marina populations (Keddy and Patriquin, 1978; Bayer, 1979; Gagnon et al., 1980; Jacobs, 1982). However, studies of structural and functional aspects of the Zostera ecosystem have generally been restricted to meadows under submerged or lower littoral conditions (e.g. Orth, 1973; Thayer et al., 1975; Lappalainen and Kangas, 1975a, 1975b; Lappalainen et al., 1977; Young and Young, 1978; Jacobs and Huisman, 1982). For this study the spatial and temporal pattern in a seagrass vegetation in the higher littoral characterized by Z. noltii and an annual form of Z. marina was investigated. The structure of a community includes the floristic and faunistic composition, the spatial and temporal patterns, the relation between the organisms and the external relations (Den Hartog, 1978, 1979). Therefore, information was gathered on qualitative and quantitative fauna parameters in addition to some abiotic characteristics, in order to elucidate some aspects of the structure and function of a community regarded as being extremely simply organized by several phytosociologists (e.g. Tüxen, 1974).

STUDY AREA

From May 1978 to April 1979 a study was carried out of a Zostera community situated on the tidal mud-flats in the southern part of the Krabbenkreek, a blind arm of the Oosterschelde (Deltaic region) in the SW of The Netherlands (see Fig. 1). The seagrass communities in this part of The Netherlands are characterized by two species belonging to the genus Zostera, i.e. Zostera marina L. and Z. noltii Hornem. The distribution and biomass of both seagrass species in the Oosterschelde were studied during a preliminary investigation in July and August of 1977. It appeared that only the bed in the southern part of the Krabbenkreek had a very high density of both species (see Fig. 1). In the area between this bed and the shore in the south (approximately 700 m) an extensive salt-marsh occurs with a typical vegetation dominated by Halimione portulacoides L., Aster tripolium L. and Limonium vulgare Mill. This salt-marsh is intersected by numerous creeks showing local luxurious stands of Zostera marina.

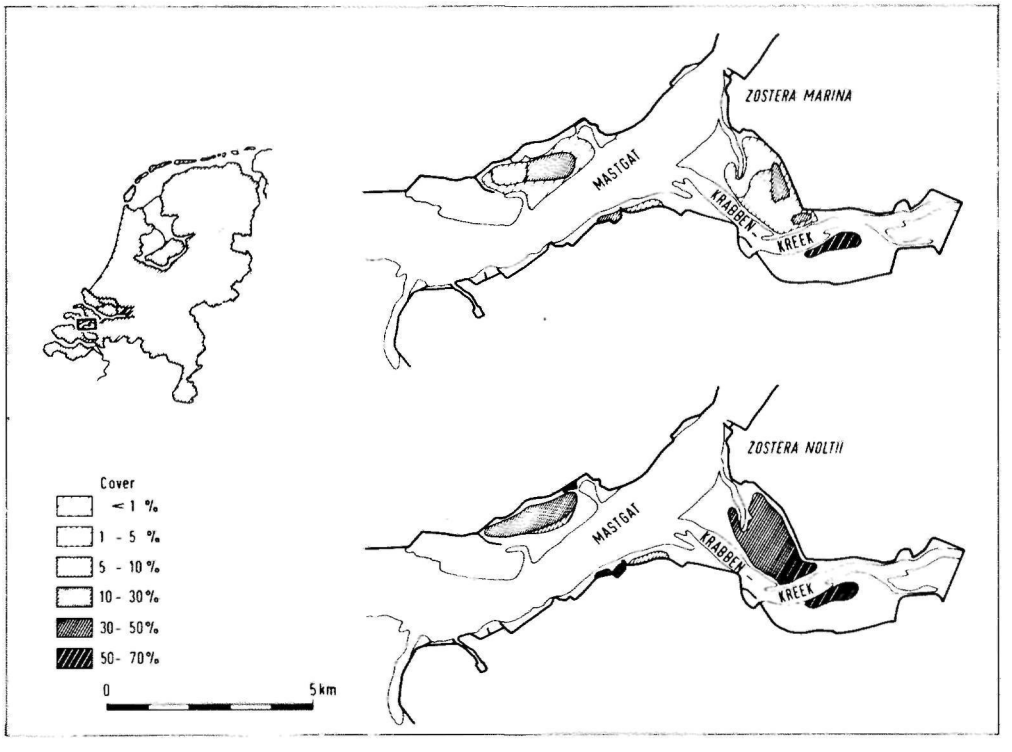


Fig. 1. Map of the Krabbenkreek with the location of the seagrass meadows. Data concerning the cover of both Zostera species represent the situation during the summer of 1977.

Two sampling stations were selected in the Zostera community: a low littoral bed and a high littoral bed. The lower bed was situated approximately 100 m to the north of the transition from salt-marsh to the mud-flat in a well-developed part of Zostera vegetation. In summer both seagrass species could be found here in high densities. The higher bed was selected near the margin of the seagrass vegetation in the south, closer to the salt-marsh in an area where Z. noltii dominated (see Table 1). The distance between the sampling stations was approximately 200 m and the difference in height was approximately 0.5 m. This difference in height was reflected by a characteristic higher water content in the bottom at the lower station, that is on average 43% of the dry weight, as compared to 30% in the higher bed. The amount of organic matter in the bottom was determined to be on average 1.7 and 1.4% of the dry weight for the lower and the higher bed, respectively. As the organic matter content and the median grain-size of the bottom are positively correlated (Newell, 1965, 1970; Longbottom, 1970), it can be concluded that the lower bed had a more muddy sediment than the higher situated bed.

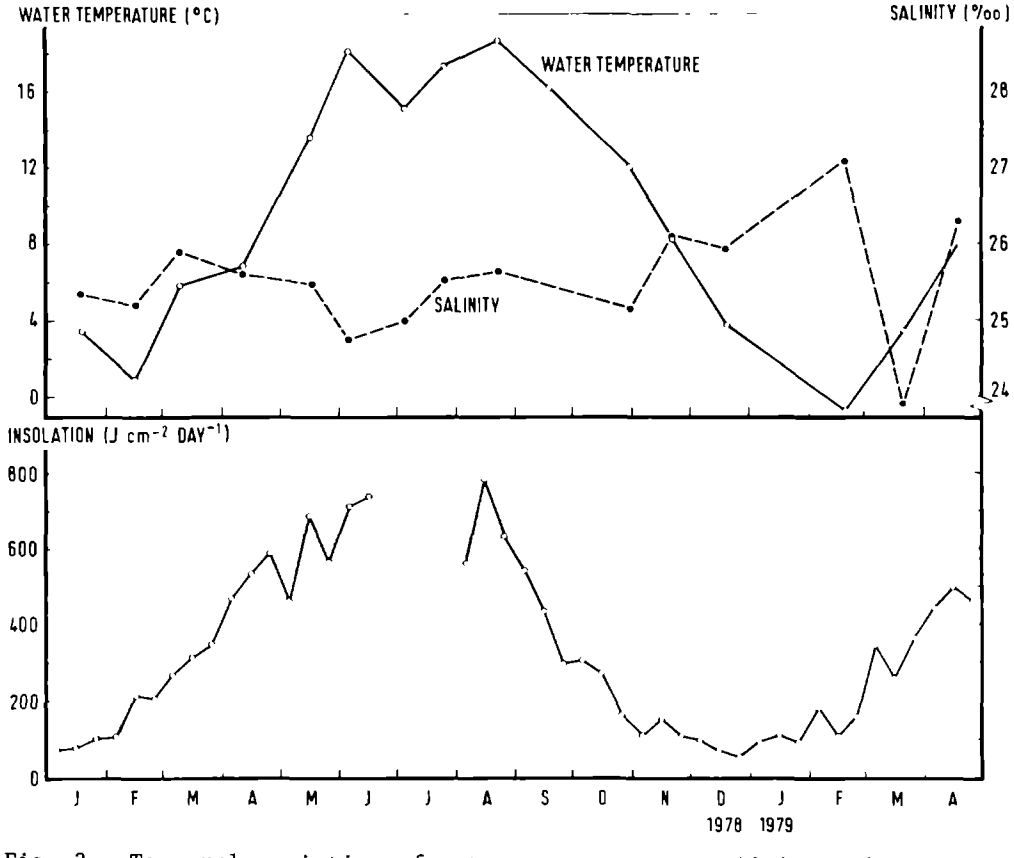


Fig. 2. Temporal variation of water temperature, salinity and insolation in the Krabbenkreek during the investigation period. Insolation data are given as mean values per 10 days of the total daily insolation characteristics.

Data concerning some abiotic factors in the Krabbenkreek were obtained from the 'Deltadienst Rijkswaterstaat' at Middelburg and are given in Fig. 2. The mean salinity measured during the investigation period was about 25.5‰, compared to 32.5‰ in the North Sea. The difference was caused by a supply of fresh water into the Krabbenkreek from the surrounding areas. This supply was nearly constant throughout the investigation period, the winter of 1978/1979 forming an exception (salinity increasing to 27‰; see Fig. 2). This exception was due to relatively low temperatures resulting in ice on inland waters. On several occasions in January and February 1979 the water temperature in the Krabbenkreek decreased to values below zero. In the same period during low tides the flats were often covered with a thin sheet of ice. Maximum temperature values were measured during the summer months: up to approximately 19°C (see Fig. 2). The insolation was measured at the 'Koninklijk Nederlands Meteorologisch Instituut' at Vlissingen, about 45 km from the study area. The total insolation per day is summarized as the mean value for each 10 day period in Fig. 2. Some data for the month of July could not be obtained due to technical difficulties.

METHODS

During the whole investigation period samples were taken around the middle of each month. In both Zostera beds the above-ground amount of seagrass was determined by estimating the percentage cover of the species and flowering was noted. Subsequently 15 random subsamples were taken from the bottom using a messing corer with a diameter of 9 cm and an area of 63.6 cm^2. Cores were driven to a depth of approximately 10 cm below the sediment surface, which depth appeared to be sufficient for reliable quantitative sampling of the bottom fauna (Wolff, 1973; F.A.A. Dubbers, personal communication, 1978). The method of random sampling is essentially the same as that described by Orth (1973). A stake was placed in each bed and was used as the centre of a circle with a diameter of 5 m. The circle was divided in 8 radial transects. A rope attached to the stake and subdivided in 10 intervals of 25 cm was moved around the perimeter of the circle using a second stake. This resulted in 80 areas which were numbered according to a distinct system. With a table of random numbers the positions of the 15 subsamples were chosen. Each core was taken to the laboratory and the fauna retained on a 0.5 mm mesh sieve was preserved in 4% formalin in sea water, sorted and identified. Subsequently all specimens of each separate species were collected from the 15 subsamples and rinsed with fresh water in order to remove adhering salt and formalin. Dry weights were determined after drying for 24 hours at 105°C. Subsequently combustion for 5 hours at 550°C gave the ash-free dry weights or 'organic content'.

Diversity indices were used to assess the diversity, i.e., Shannon's index,

$$H = -\sum_{i=1}^{S} P_i \ln P_i$$

with P_i = proportion of the abundance of species i and S = number

of species, and the evenness of H, namely $J = H / H_{max}$, where $H_{max} = \ln S$ (Pielou, 1969).

The quantitiative importance of the species, expressed as the biological index (see Fager, 1957; Sanders, 1960), was determined in each sample by giving the species a rank from 1 to 5 according to their abundance. This was carried out for numbers, dry weights and ash-free dry weights. A value of 5 points was given to the first ranking species, 4 points to the second ranking species, etc. Thus, if a species was ranked first in all samples (12 for each bed), it would have 60 points, i.e. the highest possible score, agreeing with 33.3% of the total number of points awarded per year per bed.

Distribution pattern analysis was made at each sampling date for the 15 subsamples, using the variance to mean ratio, or 'index of dispersion'. The departure from unity was assessed by reference to a table of χ^2 (Elliott, 1977).

Diversity measured by the rarefaction method (Sanders, 1968) was calculated as follows. The arithmethical means of both numbers of individuals and numbers of species of all combinations of subsamples were calculated, using an increasing sample size. Subsequently the relationships between number of species and number of individuals were determined for each sample.

Seagrass shoots or parts of these in the subsamples, were collected per sample and divided into above-ground and below-ground plant parts by sectioning through the meristematic region. When a sample contained weighable quantities, the total was rinsed in fresh water, dried at 105°C (24 hours), followed by combustion at 550°C (3 hours) in order to determine dry weights and ash-free dry weights. As fragments of the two Zostera species could not be identified and separated, the data are given as total seagrass biomass of an area of 15 x 63.6 cm^2 = 954 cm^2; this is converted to values per m^2.

RESULTS

1. STRUCTURE AND DYNAMICS OF THE VEGETATION

The seagrass meadow in the Krabbenkreek was characterized during summer by two species, i.e. Zostera marina and Z. noltii. However, from January to April only the smaller seagrass, Z. noltii, was found. This is clearly expressed by the cover percentages in Table 1, which include the temporal changes in abundance of the above-ground plant parts of both species. These data clearly show the lowest cover percentages in the high littoral bed near the margin of the meadow. Z. marina was represented there by scattered growing plants, forming a very low cover. Even the cover of Z. noltii was less than that in the lower bed, reaching a maximum value of only 35%.

From the data in Table 1 it can be deduced that the two seagrasses were characterized by a short growing season. From May onwards the cover increased reaching a maximum in August/September, declining to almost zero in November/December. Generative shoots of both species were found from July to October, with a maximum in August, when all the shoots in the lower bed were flowering.

TABLE 1

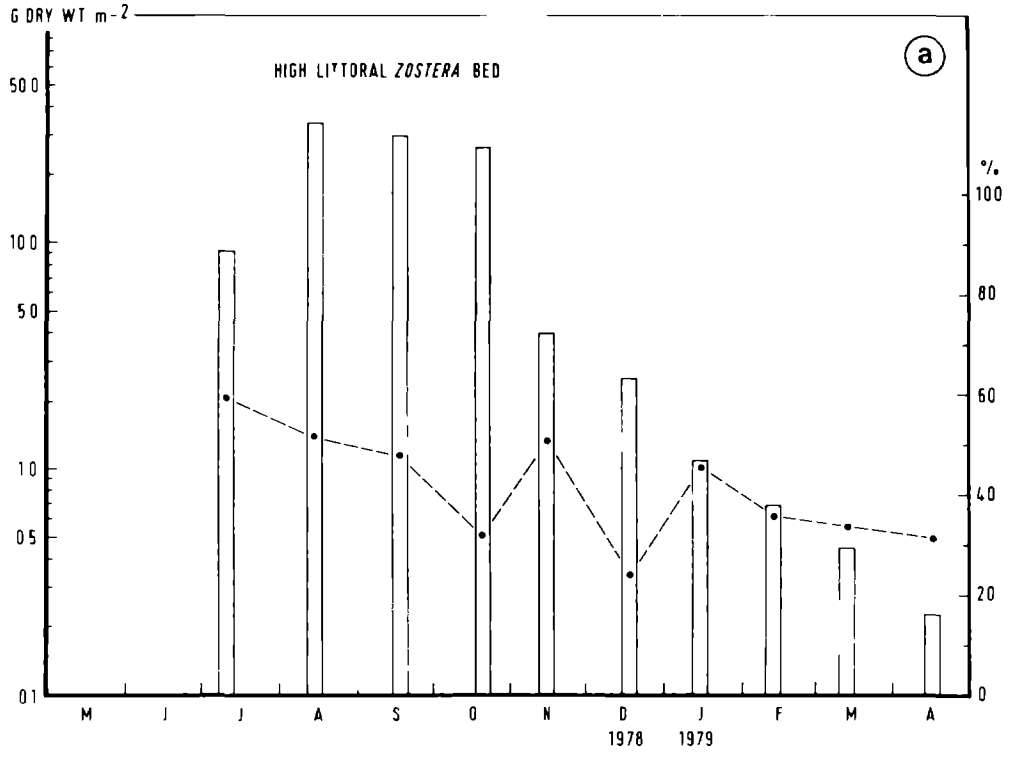
Seasonal variation in cover (given as percentages) of the two Zostera species at the sampling stations in the Krabbenkreek.

Sampling date	High littoral Zostera bed		Low littoral Zostera bed	
	Z. marina	Z. noltii	Z. marina	Z. noltii
May 1978	0	<1	<1	<1
June	0	<1	1 - 5	<1
July	<1	5	15 - 20	5 - 10
August	<1	25 - 35	50 - 75	30 - 40
September	1 - 5	10 - 20	50 - 60	60 - 70
October	<1	10 - 15	10 - 15	10 - 15
November	<1	1 - 5	1 - 5	1 - 5
December 1978	0	1 - 5	0	1 - 5
January 1979	0	1 - 5	0	1 - 5
February	0	<1	0	<1
March	0	<1	0	<1
April 1979	0	<1	<1	<1

Macroalgae were found between the seagrass shoots in particular during the summer months. The network of the sometimes thick mat consisted of loose lying interwoven filaments of Chaetomorpha linum Kütz. This mat sometimes also contained species such as Fucus spp. and Ulva lactuca L.

The total biomass of both Zostera species showed considerable variation during the year (see Fig. 3). The maximum value for the higher bed was 34 g dry wt m^{-2} (in August) and for the lower bed 94 g dry wt m^{-2} (in September).

The minimum values were found in April in the higher bed (0.239 g dry wt m^{-2}) and in March in the lower bed (0.073 g dry wt m^{-2}). As the vegetation of the higher bed was almost completely dominated by Z. noltii (see Table 1), the biomass data therefore approximately represent the characteristics of this seagrass species. During almost the whole investigation period the share of the above-ground plant biomass in the higher bed was lower than 50% of the total dry weight (see Fig. 3), decreasing slowly after the end of the growing season. Consequently decreasing cover percentages did not coincide with a decreasing biomass of the rhizomes and roots. Apparently the below-ground plant parts overwintered and only a very small standing


G DRY WT m-2
HIGH LITTORAL ZOSTERA BED
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100
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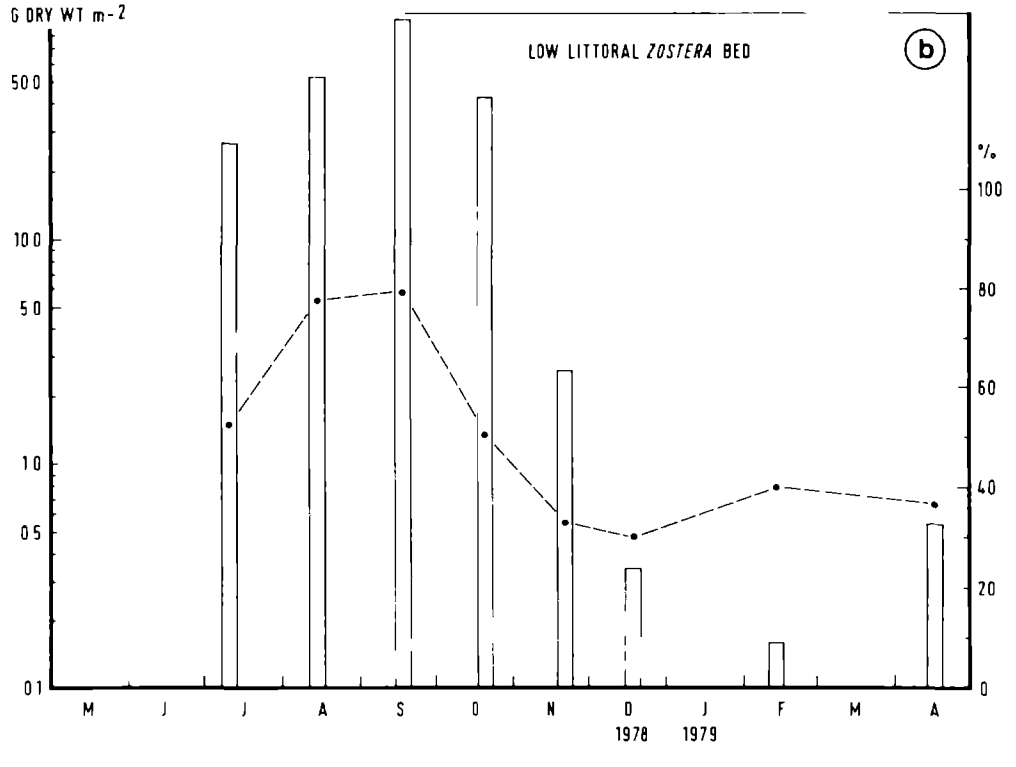
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crop of leaves of Z. noltii was found during the winter period. The biomass in terms of ash-free dry weight of the above-ground plant parts was on average 78.2% of the dry weight for the whole period; for the rhizomes and roots this percentage was 69.3%.

In comparison with the higher bed, the lower seagrass bed showed a heavier biomass during summer and a lighter one during winter (see Fig. 3). These differences were apparently caused by a higher proportion of Z. marina in the vegetation, illustrated by the very high cover in the lower bed. In the period with high densities (July to October, see Table 1) the contribution of the above-ground parts amounted to approximately 80% of the total biomass. This percentage decreased during winter to values comparable with the percentages for the higher bed, i.e. for a typical Z. noltii vegetation. As all the shoots of Z. marina flowered during summer, the major part of the above-ground biomass in the lower bed was composed of the axes of the generative shoots with rhipidia and leaves, only a smaller part being formed by the rhizomes and roots. The ash-free dry weight (as the average percentage of the dry weight over the whole investigation period) approximated the values for the higher bed and amounted to 75% and 65% of the dry weights of the above-ground and the below-ground plant parts, respectively.

2. STRUCTURE AND DYNAMICS OF THE INHABITING MACROFAUNAL COMMUNITY

QUANTITATIVE STRUCTURE AND SPECIES DIVERSITY

The macrofaunal characteristics of both Zostera beds are summarized in Fig. 4. Besides the total numbers of individuals and the species richness, the values for diversity and evenness are given.

A total of 360 cores taken during the whole investigation period yielded 20,609 and 25,817 individuals for the higher and the lower bed respectively, together belonging to 35 taxa. For the higher bed the mean numbers of species and of individuals m^{-2} were computed as 19.8 and 17,998, respectively. The total number of species ranged from 15 to 23 with lowest values in spring (Fig. 4a). Calculations for the lower bed resulted in mean numbers per square metre of 19.3 species and 22,545 individuals; the total number of species found per sample ranged from 15 to 23 (Fig. 4b).

Considering the numbers of species and of individuals during the year, the fluctuations were significant. Nevertheless, in general the fauna of the lower bed appeared to show a greater number of species and of individuals.

Fig. 3. Seasonal variation in the total Zostera biomass (histogram) in the seagrass beds; the percentage of the above-ground plant parts is shown by the broken line.

Temporal changes in abundance and species richness resulted in differences between the diversity indices of the samples. In the higher bed the index ranged from 1.22 to 1.98 (av. 1.58) and for the lower bed from 1.07 to 1.80 (av. 1.45). Values for the evenness were computed between 0.40 and 0.64 (av. 0.53) for the higher bed and between 0.38 and 0.60 (av. 0.49) for the lower bed. Analysis of the diversity with respect to the course of the indices during the year, gave conspicuous differences between the two sites. Values for the lower bed showed remarkable variability, whereas for the higher bed a more regular course was found with maximum scores in summer. From these patterns it can be concluded that the higher bed gave evidence of higher stability in a more diverse community.

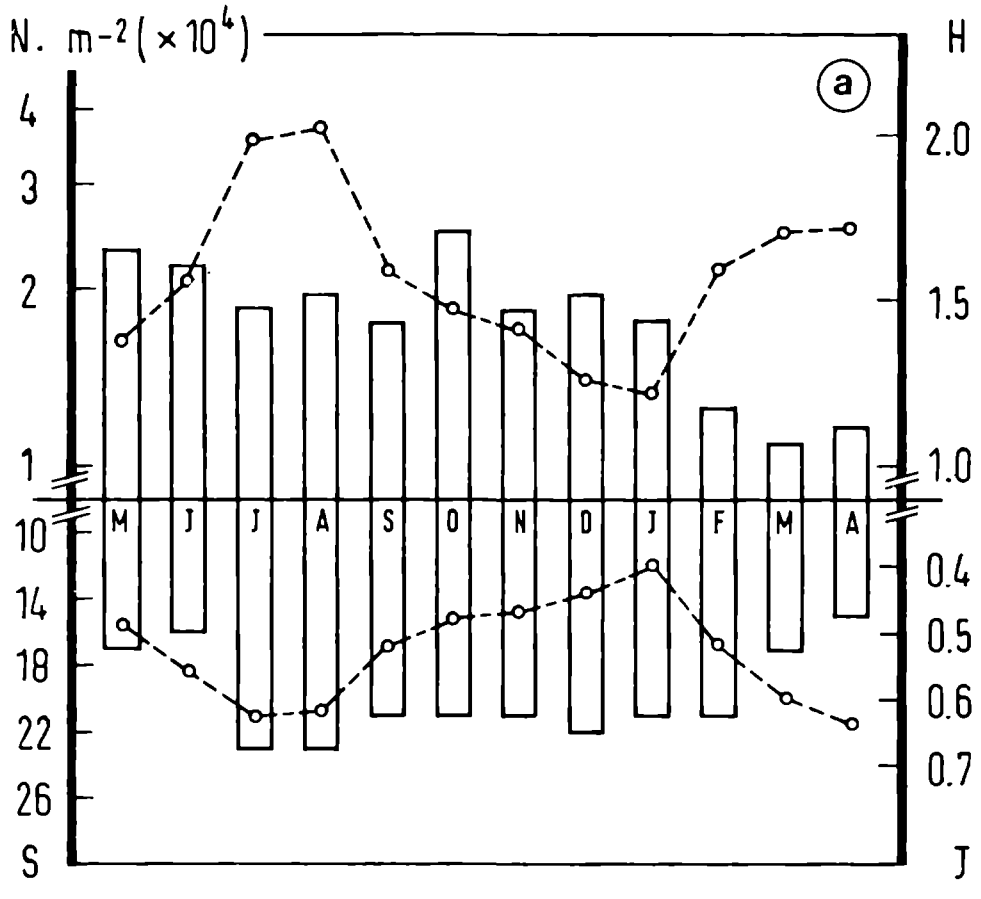

Fig. 4a. See legend on facing page.

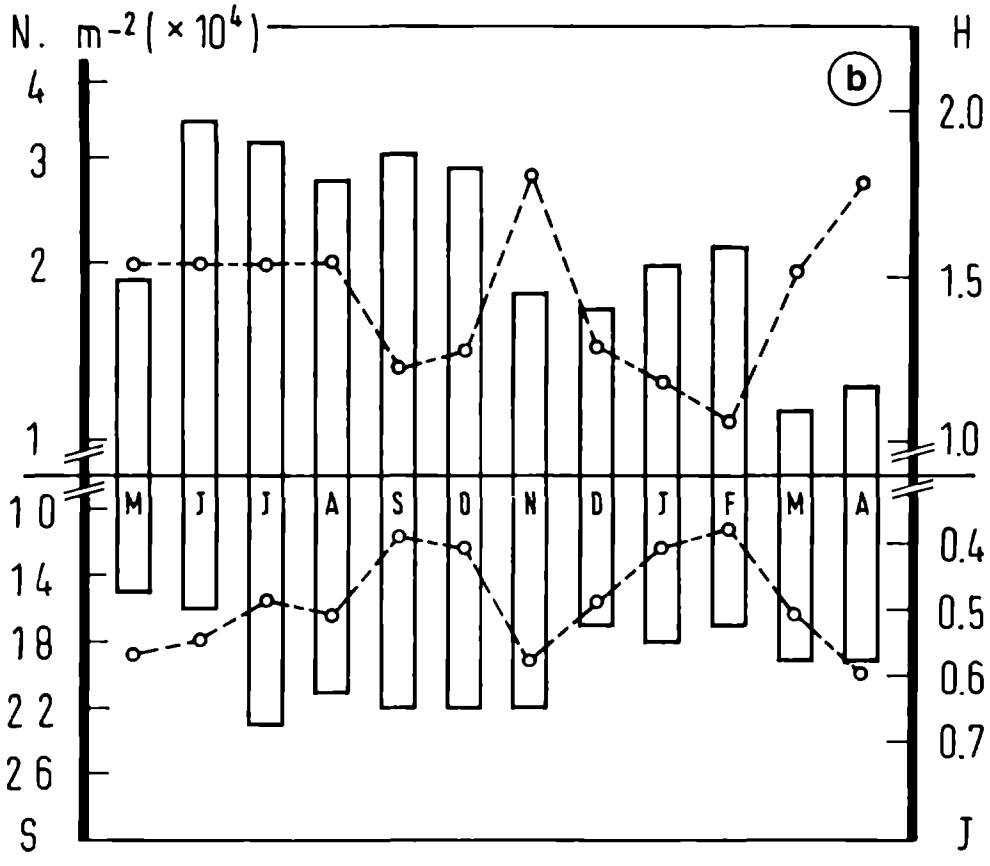

Fig. 4b. Quantitative characteristics of the macrofauna of the Zostera community in the Krabbenkreek, sampled from May 1978 to April 1979; (a) high and (b) low littoral Zostera bed (N = number of individuals; S = number of species; H = diversity index (broken line); J = evenness (broken line)).

Diversity measured by the rarefaction method (Sanders, 1968), allows direct comparison of samples with differing numbers of individuals. This can be regarded as a summary of the quantitative results. For each discrete sample a specific relationship was computed between species richness (S) and species abundance (N) (Table 2). From the extracted r-values, ranging from 0.97 to 0.99, it can be concluded that these parameters were highly correlated. Subsequently compiled S for a specific N, resulted in an equalization of the samples, implicating that differences in species richness were only dependent on the month in which sampling took place. These temporal variations indicated some differences existing between scores in summer / autumn and winter / spring. However, higher scores could be

assigned to rare species, collected in only one of the subsamples. In addition, if the calculated species richness is only calculated at lower N values, these numbers might be underestimated (see Table 2 for N = 500 and N = 1000). Nevertheless, this richness appeared to be a realistic approximation of the numerical correlation at lower abundance. However, actual comparison was only realistic at the saturation level of the species accumulation curves. These curves were generated for all cores of each sample using the method of sample accumulation. In addition to the regression characteristics given in Table 2, some examples of the resulting curves are shown in Fig. 5. For all samples a rapid initial increase in species richness was found for numbers of individuals up to 500 and nearly all curves showed an approximate saturation level at numbers between N = 1000 and N = 2000. Since the number of individuals collected with the samples (on average 1717 (SD = 421) and 2151 (SD = 743) in the higher and lower bed respectively) fell within the numbers determining the saturation levels, the sampling method appeared to be very efficient. Thus, it can be concluded that the number of subsamples (i.e. 15, agreeing with an area of 954 cm^2) was optimal for a collection containing the majority of the species, although differences in species composition were observed among the subsamples.

From the form of the saturation curves it can be derived that the asymptotic levels (calculated from the data in Table 2) were correlated with the time of sampling. The highest levels were found from July 1978 to February 1979 in the higher seagrass bed, and from July 1978 to November 1978 in the lower bed. Since samples characterized by one or more dominant species, i.e. a high N/S ratio, show a relatively lower diversity and a lower asymptotic level, the highest diversity of the faunal assemblages was recorded in the above mentioned periods.

SPECIES COMPOSITION AND DOMINANCE

All taxa found in the samples collected from the two seagrass beds are listed in Table 3. In addition, this 'presence-table' gives an indication of the abundance of the recorded species. The species composition of both sampling stations appeared to be very similar and comparable. Within the faunal assemblage inhabiting the Zostera beds three major groups can be distinguished.

(1) Benthic infaunal species and mobile species occurring in as well as outside the vegetation. These animals were found in nearly all samples and generally in great numbers. This group included species characteristic for high littoral intertidal flats (see also Wolff, 1973; Reise, 1978; Jacobs and Huisman, 1982). Most of these animals were resident infaunal species, living in the bottom or just below the bottom surface (e.g. dense infaunal assemblage of deposit-feeding, tube-building polychaetes). In addition, the mudsnails (Hydrobia ulvae) and the periwinkles (Littorina littorea) contributed to the quantitiative importance of this group.

TABLE 2

Temporal variation in regression characteristics of the relation between mean numbers of species (S) and numbers of individuals (N) of the fauna in the two Zostera beds, according to the formula S = a log N + b, and the subsequently calculated numbers of species for N = 500, N = 1000 and N = 2000.

Sampling date	High littoral Zostera bed					Low littoral Zostera bed				
	Regression characteristics		Calculated S for N =			Regression Characteristics		Calculated S for N =		
	Slope (a)	Intercept (b)	500	1000	2000	Slope (a)	Intercept (b)	500	1000	2000
May 1978	6.35	-3.96	13.3	15.2	17.1	4.54	+0.64	12.9	14.3	15.6
June	5.34	-1.41	13.0	14.6	16.2	4.59	+0.23	12.6	14.0	15.4
July	8.13	-3.05	18.9	21.3	23.8	9.05	-8.43	16.0	18.7	21.4
August	8.60	-5.17	18.0	20.6	24.7	6.83	-1.80	16.6	18.7	20.7
September	7.22	-1.76	17.7	19.9	22.1	8.50	-6.53	16.4	19.0	21.5
October	7.24	-2.61	16.9	19.1	21.3	9.24	-9.96	15.0	17.7	20.5
November	9.07	-7.92	16.6	19.3	22.0	9.13	-7.14	17.5	20.3	23.0
December 1978	10.40	-11.73	16.3	19.5	22.6	6.82	-5.30	13.1	15.2	18.4
January 1979	10.72	-13.33	15.6	18.8	22.1	8.10	-8.71	13.2	15.6	18.0
February	10.91	-12.36	17.1	20.4	23.7	7.40	-8.10	11.9	14.1	16.3
March	7.18	-4.09	15.3	17.5	19.6	9.63	-10.64	15.3	18.2	21.1
April 1979	4.92	+0.35	13.6	15.1	16.6	8.27	-6.53	15.8	18.3	20.8

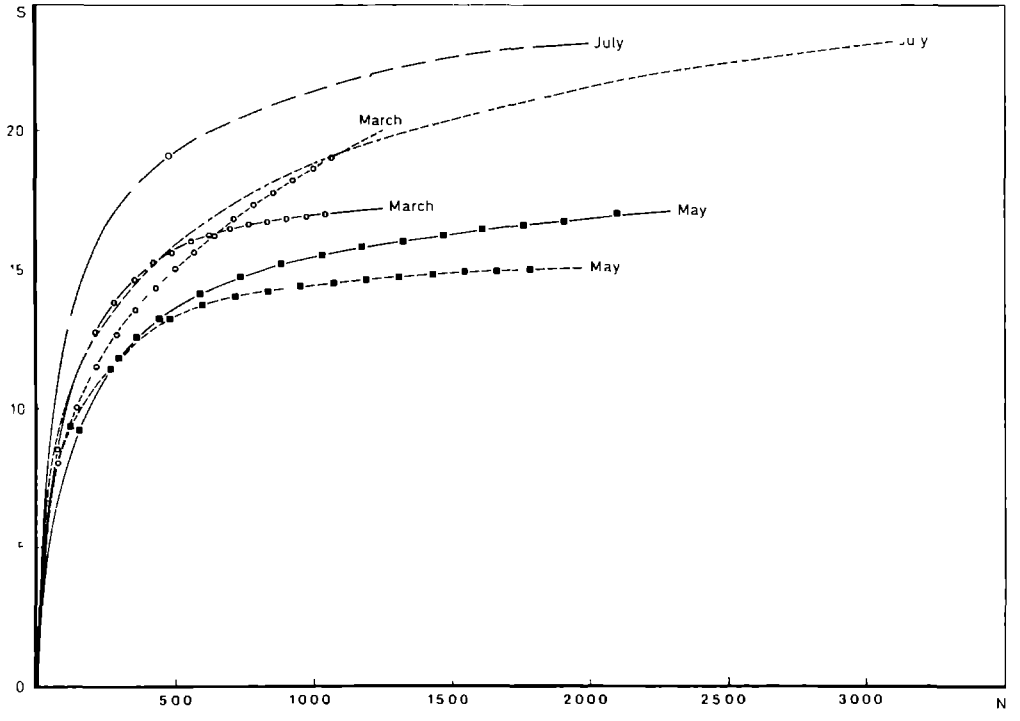

Fig. 5. Some rarefacted diversity curves for the benthic fauna of both Zostera beds in the Krabbenkreek; straight line: high littoral bed; broken line: low littoral bed (N = number of individuals, S = number of species).

(2) Species which seemed to be structurally related to the vegetation or which have the same life cycle as Zostera. These species were responsible for the temporal fluctuations in species richness and formed a smaller part of the species list. They were recorded from July onwards and appeared to be most numerous during summer and autumn, followed by a decrease during winter. This pattern was most conspicuous for the samples taken in the higher bed (see Table 3a). In this temporary group of animals the numbers scored showed a strong correlation to the presence of seagrass in the samples (see Fig. 3 and Table 1). The plant beds apparently offered a special habitat for these species, mainly belonging to Crustacea and Polychaeta Errantia.

(3) The third group of species consisted mainly of incidental inhabitants, not characteristic for this habitat. Their presence was most likely due to invasion from surrounding brackish and fresh waters. These species are mentioned in the lower parts of the Tables 3a and 3b.

From this analysis of the macrofauna species composition it can be concluded that the presence of suitable habitats may be responsible for the permanent or temporary occurrence of species. This also explains the differences between the Tables 3a and 3b with respect to the species composition of the 3 groups.

Numerical analysis, however, demonstrates a different phenomenon. This is summarized in Table 4, which gives the seasonal biological index for the five dominant fauna species found in each sample. Examination of the relative biological index values and the frequency of scoring, only shows resident species in the first group, while Anaitides maculata and Gammarus crinicornis belong to the second group. From the data in Table 4 it can be concluded that these numerically important species represented a characteristic and constant part of the faunal assemblage.

FAUNAL BIOMASS AND DOMINANCE

The biomass of the faunal assemblages in terms of dry weight and ash-free dry weight was computed for each separate sample by adding the weights of all specimens of each species.

In the higher bed the total animal biomass ranged from 25.8 to 177.0 (average 111.4) g dry wt m^{-2} (see Fig. 6a). The data presented in Table 4 provide evidence that certain species dominated. Over the whole year only two species, i.e. Hydrobia ulvae and Cerastoderma edule, made up 72% of the biomass, while the Mollusca together comprised 90% of the total quantity of living organisms. Only a few other numerically more abundant species contributed significantly to the biomass (Scoloplos armiger, Arenicola marina and Nereis diversicolor). The overwhelming dominance of the Mollusca determined the major trends of the diversity indices, shown in Fig. 6. As a direct consequence of this dominance the diversity values were relatively low: H ranged from 1.21 to 1.92 (average 1.48) and J ranged from 0.31 to 0.71 (average 0.50).

Comparing the faunal biomass in terms of dry weights recorded in both Zostera beds, the values for the lower bed appeared to be considerably higher with a mean value for all 12 samples of 181.7 g dry wt m^{-2} (minimum 85.8, maximum 304.4). As distinct from the situation in the higher bed, the biomass of Littorina littorea contributed significantly to the total biomass. Together with Hydrobia ulvae and Cerastoderma edule this gastropod represented an average of 88% of the total dry weights. Analysis of the biomass according to dominance (Table 4), demonstrated the particular importance of the Mollusca, corresponding to an average share of 97% of the total biomass. This indicates that this group determined the ultimate fluctuations during the year, illustrated in Fig 6b. Moreover, the dominance is also expressed in low diversity values: H ranged from 1.16 to 1.70 (average 1.34) and J ranged from 0.37 to 0.58 (average 0.46).

As biomass is defined as the amount of living material, it seems to be more convenient to express biomass in a more refined manner by excluding those parts of the animals that are non-living (Crisp, 1971). After drying and subsequently combusting, the ash-free dry

TABLE 3a

Macrofaunal taxa collected in the high littoral (a) and low littoral (b) seagrass bed in the Krabbenkreek (1 = 10-100 ind.m^{-2}; 2 = 100-500 ind.m^{-2}; 3 = 500-1000 ind.m^{-2}; 4 = 1000-5000 ind.m^{-2}; 5 =>5000 ind.m^{-2}), showing the groups characteristic for the high littoral tidal flats, for the seagrass bed, and formed from incidental inhabitants.

Month	M	J	J	A	S	O	N	D	J	F	M	A
	1978								1979			
Hydrobia ulvae (Pennant) (G)	5	5	5	5	5	5	5	5	5	5	4	4
Peloscolex benedeni Udekem (O)	5	5	4	4	4	4	4	4	4	4	4	5
Scoloplos armiger (Müller) (PS)	4	4	4	4	4	4	4	4	4	4	4	4
Capitella capitata (Fabricius) (PS)	4	4	4	4	3	3	3	3	1	2	2	2
Heteromastus filiformis (Claparède) (PS)	2	2	3	3	2	2	2	2	3	3	3	3
Tubificidae spp. (O	3	1	3	3	2	2	2	3	2	2	2	2
Eteone longa (Fabricius) (PE)	2	2	3	3	3	3	2	2	2	2	2	2
Macoma balthica (Linnaeus) (B)	1	2	2	2	2	2	1	2	2	1	1	1
Arenicola marina (Linnaeus) (PS)	2	2	2	2	1	2	2	1	1	1	1	1
Pygospio elegans Claparède (PS)	1	2	3	2	1	2	1	1	1	1	1	2
Cerastoderma edule (Linnaeus) (B)	1	1	2	2	2	2	2	2	2	1	1	
Corophium volutator (Pallas) (A)	1	1	2	1	1	2	1	2	1	1	1	2
Scrobicularia plana (Da Costa) (B)	1	1	1	1	1	1	1	1	1	1	1	1
Nereis diversicolor (Müller) (PE)	2	2	2	1	1			1	1	1	2	2
Tharyx marioni (Saint Joseph) (PS)	1		1	1	1		1		1	1	1	1
Littorina littorea (Linnaeus) (G)		1	1	1	1	2	1	1	1	1		1
Anaitides maculata (Linnaeus) (PE)			2	3	2	3	2	1	1		1	
Retusa obtusa (Montagu) (G)			2	2	2	1	1	1	1	1	1	
Carcinus maenas (Linnaeus) (D)			2	2		1		1	1			
Crangon crangon (Linnaeus (D)			1	2	1	1	1					
Idotea chelipes (Pallas) (I)				1	1	1	1	1		1		
Lineus sp. (N)				1	1	1	1	1	1	1		
Hyale nilssoni (Rathke) (I)				1				1				
Gammarus crinicornis Stock (A)						4	1					
Nephtys hombergii (Savigny) (PL)	1											
Golfingia sp. (S)			1									
Turbellaria			1									
Chironomus sp. (H)								1				
Paragnathia formica (Hesse) (I)										1		
Syntormon zelleri Loew (H)	1	1	1						1	1		

TABLE 3b

See legend on facing page.

Month	M	J	J	A	S	O	N	D	J	F	M	A
	1978								1979			
Hydrobia ulvae (Pennant) (G)	5	5	5	5	5	5	5	5	5	5	5	4
Peloscolex benedeni Udekum (O)	4	4	4	4	4	4	4	4	4	4	4	4
Tharyx marioni (Saint Joseph) (PS)	4	4	4	4	4	4	4	4	3	3	3	3
Scoloplos armiger (Müller) (PS)	3	4	4	4	3	3	3	3	4	3	3	2
Tubificidae spp.* (O)	3	4	3	2	3	4	4	4	3	3	2	3
Heteromastus filiformis (Claparède) (PS)	2	3	3	3	3	2	3	2	2	2	3	3
Eteone longa (Fabricius) (PE)	2	2	2	2	2	1	1	2	2	2	2	2
Littorina littorea (Linnaeus) (G)		1	1	2	3	3	3	2	2	2	2	1
Cerastoderma edule (Linnaeus) (B)	1	2	2	3	2	2	2	2	2	1	1	1
Pygospio elegans Claparède (PS)	3	4	4	2	1	1	1		1	1	1	1
Capitella capitata (Fabricius) (PS)	2	1	2	1	2	2	2	1		1	1	2
Nereis diversicolor (Müller) (PE)	1	1	2	2	1	1	1	1	1		1	2
Scrobicularia plana (Da Costa) (B)	1	1	1	1	1	1	1	1	1	1	1	1
Macoma balthica (Linnaeus) (B)	1	1	1	1	1	1	1	1	1	1	1	1
Arenicola marina (Linnaeus) (PS)	1	1	1		1				1	1	1	1
Anaitides maculata (Linnaeus) (PE)			2	2	2	3	2	1	1	1	1	1
Idotea chelipes (Pallas) (I)			1	2	1	?	1	1	1		1	1
Carcinus maenas (Linnaeus) (D)			1	2	?	1	1		1			
Gammarus crinicornis Stock (A)				1	2	3	2	1				
Retusa obtusa (Montagu) (G)			1	2	1						1	
Crangon crangon (Linnaeus) (D)			1	1	1							
Corophium volutator (Pallas) (A)		1					1		1	1		
Nephtys hombergii (Savigny) (PE)	1		1			1	1					
Lineus sp. (N)						1	1				1	1
Syntormon zelleri Loew (H)												1
Golfingia sp. (S)			1									
Anurida maritima (Guérin) (C)				1	1							
Hyale nilssoni (Rathke) (A)								1				
Chironomus sp. (H)										1		
Ampharete acutifrons (Grube) (PS)			1									
Polydora quadrilobata Jacobi (PS)						1						
Polydora ligni Webster (PS)						1						
Lanice conchilega (Pallas) (PS)							1					

A = Amphipoda; B = Bivalvia; C = Collembola; D = Decapoda; G = Gastropoda; H = Hexapoda; I = Isopoda; N = Nemertini; O = Oligochaeta; PE = Polychaeta Errantia; PS = Polychaeta Sedentaria; S = Sipunculida.

* including Tubifex pseudogaster (Dahl)

TABLE 4

Total seasonal biological index for the five dominant fauna species found in each sample taken in the Zostera beds and their feeding type. The index is calculated for numbers, dry weights and ash-free dry weights and is given as a percentage of the total score for each category with a highest possible score of 33.3% for each species. Frequency of scoring (in number of months) is given in parentheses.

Species	High littoral Zostera bed			Low littoral Zostera bed			Feeding type **
	Numbers	Dry wt.	Ash-free dry wt.	Numbers	Dry wt.	Ash-free dry wt.	
Pygospic elegans (PS)*	0.6 (1)			0.6 (1)			2a - 1
Scoloplos armiger (PS)	19.4 (12)	8.3 (9)	22.2 (12)	10.5 (10)	1.1 (2)	3.9 (5)	2b
Arenicola marina (PS)		1.7 (2)	2.8 (4)		0.6 (1)	1.7 (1)	2b
Capitella capitata (PS)	10.0 (9)						2b
Heteromastus filiformis (PS)	4.5 (4)			2.2 (3)	1.6 (2)	7.2 (8)	2b
Tharyx marioni (PS)				17.8 (12)			2a
Anaitides maculata (PE)	1.1 (2)		1.1 (1)	0.6 (1)		0.6 (1)	3 - 4
Nereis diversicolor (PE)		2.8 (2)	8.3 (5)		0.6 (1)	3.3 (2)	6
Eteone longa (PE)	1.1 (2)						4
Peloscolex benedeni (O)	27.2 (12)		0.6 (1)	24.4 (12)			2
Tubificidae spp. (O)	2.8 (5)			10.0 (8)			2
Carcinus maenas (D)					0.6 (1)	0.6 (1)	4
Gammarus crinicornis (A)	1.1 (1)						6
Hydrobia ulvae (G)	32.2 (12)	29.4 (12)	29.4 (12)	33.3 (12)	30.5 (12)	32.7 (12)	2 - 5
Littorina littorea (G)		2.2 (3)		0.6 (1)	16.7 (10)	14.4 (8)	5
Cerastoderma edule (B)		27.8 (11)	21.7 (11)		27.8 (12)	23.9 (12)	1
Scrobicularia plana (B)		17.2 (11)	10.6 (10)		15.5 (12)	11.1 (9)	2a - 1
Macoma balthica (B)		10.6 (10)	3.3 (4)		5.0 (7)	0.6 (1)	2

*PS = Polychaeta Sedentaria; PE = Polychaeta Errantia; O = Oligochaeta; D = Decapoda; A = Amphipoda; G = Gastropoda; B = Bivalvia.

**1 = suspension-feeders; 2a = selective deposit-feeders; 2b = non-selective deposit-feeders; 3 = scavengers; 4 = carnivores; 5 = herbivores; 6 = omnivores.

organic matter, which is regarded as a good parameter of the living substance, can be calculated. The mass of living tissue of the fauna, found in each sample, is shown in Fig. 7. For the higher seagrass bed these biomass values ranged from 8.3 to 23.8 (average 14.8) g ash-free dry wt m^{-2} and for the lower bed from 12.3 to 36.0 (average 20.1). Inherent to this specific biomass determination is the exclusion of the weights of the mollusc shells. This resulted in a diminished dominance of this group of animals, although their average percentage composition, over the whole year, still amounted to 65% for the higher bed and to 81% for the lower bed. This means that some numerically more abundant species (e.g. Scoloplos armiger and Heteromastus filiformis) and Arenicola marina, Nereis diversicolor and Carcinus maenas, because of their large individual size, represented important biomass components of the ash-free dry weights (see Table 4). However, of the numerically dominant species listed in Table 4, only Scoloplos armiger and Hydrobia ulvae had high mean total biological indices for the biomass. In comparison to the dry weights, these patterns demonstrated a more equal distribution of the ash-free dry weights over the species, expressed by relatively higher mean diversity values; the higher bed H ranged from 1.57 to 2.24 (average 1.91) and J from 0.51 to 0.75 (average 0.64). For the lower bed the average H was 1.73 (extreme values: 1.42 and 2.11) and the average value for J was 0.59 (extreme values: 0.50 and 0.71) (see Fig. 7).

SPATIAL DISTRIBUTION

The spatial distribution of a population describes the spatial pattern of the individuals of a species in a definite area. This information may attribute to quantitative ecological information, such as abundance, biomass etc. Three basic distribution types are distinguished, i.e. regular, random and contagious. These types can overlap, e.g. a contagious distribution can result from randomly-distributed groups. The detection of each pattern will depend upon the size of the sampling unit (Rosenberg, 1974, 1977; Elliott, 1977) and also upon the distribution of environmental factors, inter- and intraspecific relationships, etc.

The analyses of the spatial distributions, summarized over the whole year for each species, brought to light some remarkable features. In general the numerically dominant species mentioned in Table 4, were mostly contagiously distributed. However, some of these species e.g. Scoloplos armiger, Heteromastus filiformis and Eteone longa, occasionally showed a tendency towards a regular or random distribution. Apparently the dominant species were not always contagiously distributed in the same manner within the same habitat and the patterns of a particular species varied within a small area or in time. Probably all these species occurred in large clumps with individuals randomly or uniformly distributed in each clump. The final recorded pattern, determined by the size of the sampled clumps and the distribution of the specimens within the clumps, resulted from patches of very high densities (clumps) on a background of low density, apparently caused by the varying composition of the substrate. This explanation seems to be quite reasonable, for the

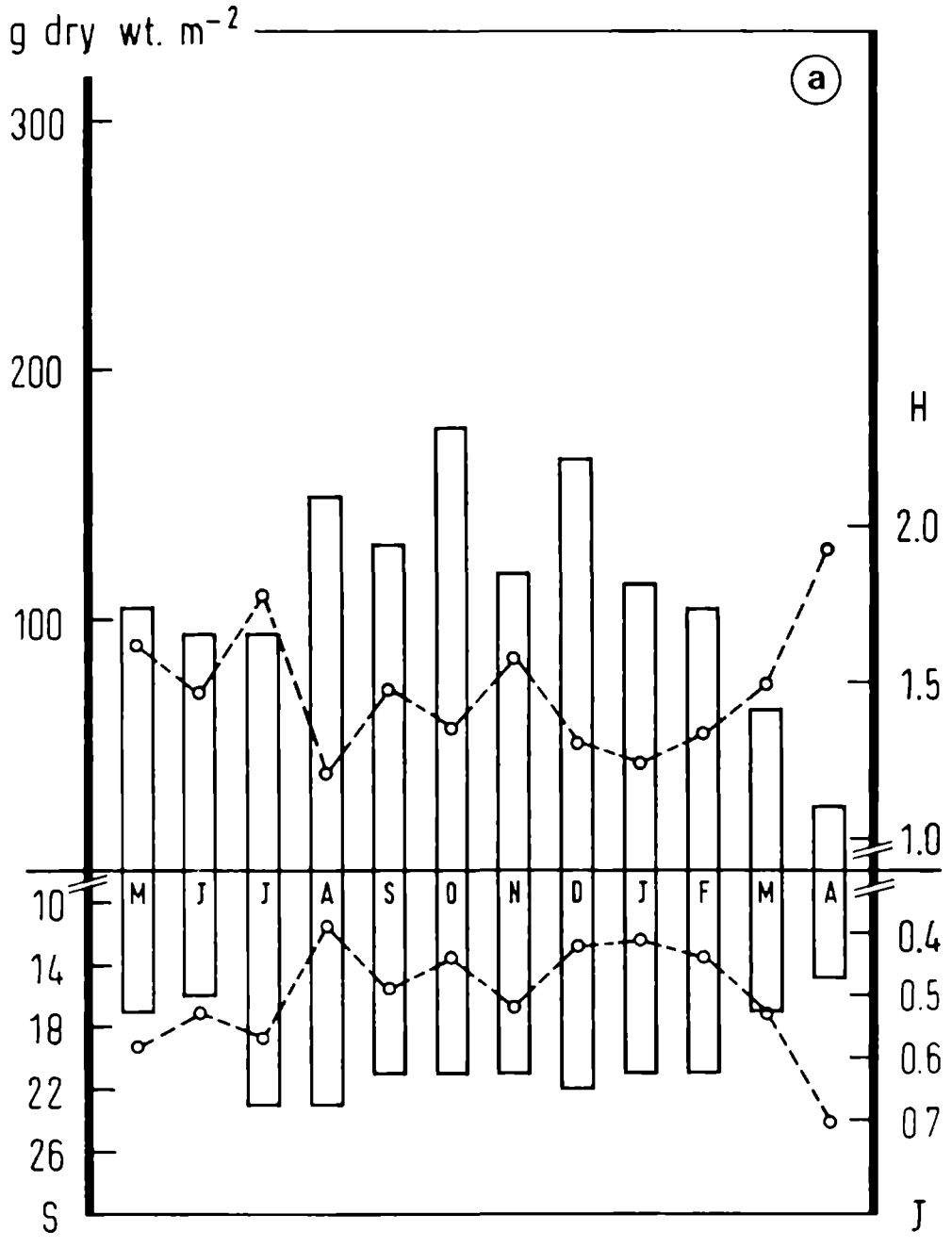

Fig. 6a. See legend on facing page.

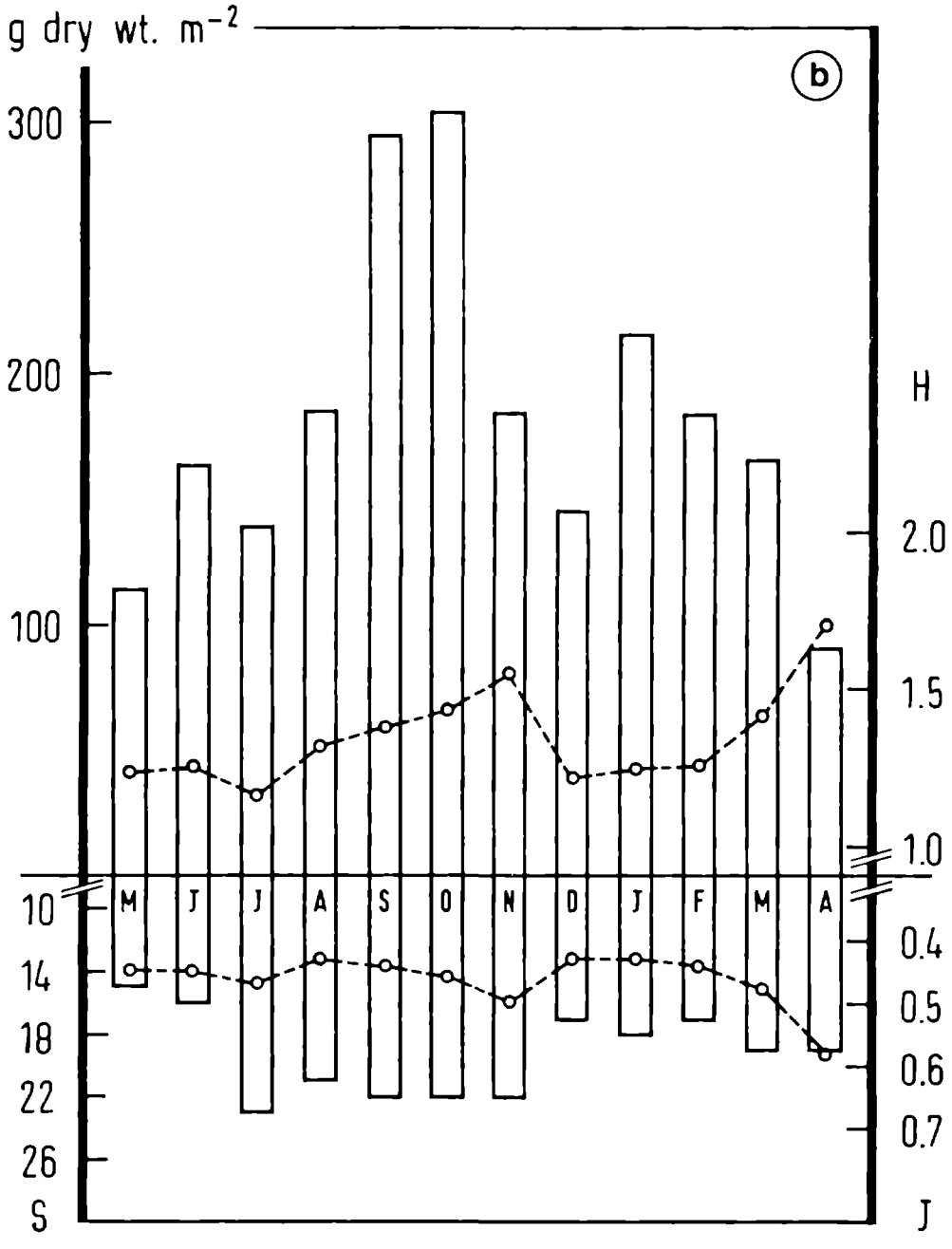

Fig. 6b. Seasonal variations of macrofaunal dry weights in the samples taken in the high (a) and (b) low littoral Zostera bed in the Krabbenkreek and the relations between species richness and biomass, expressed as diversity (S = number of species; H = diversity index (broken line); J = evenness (broken line)).

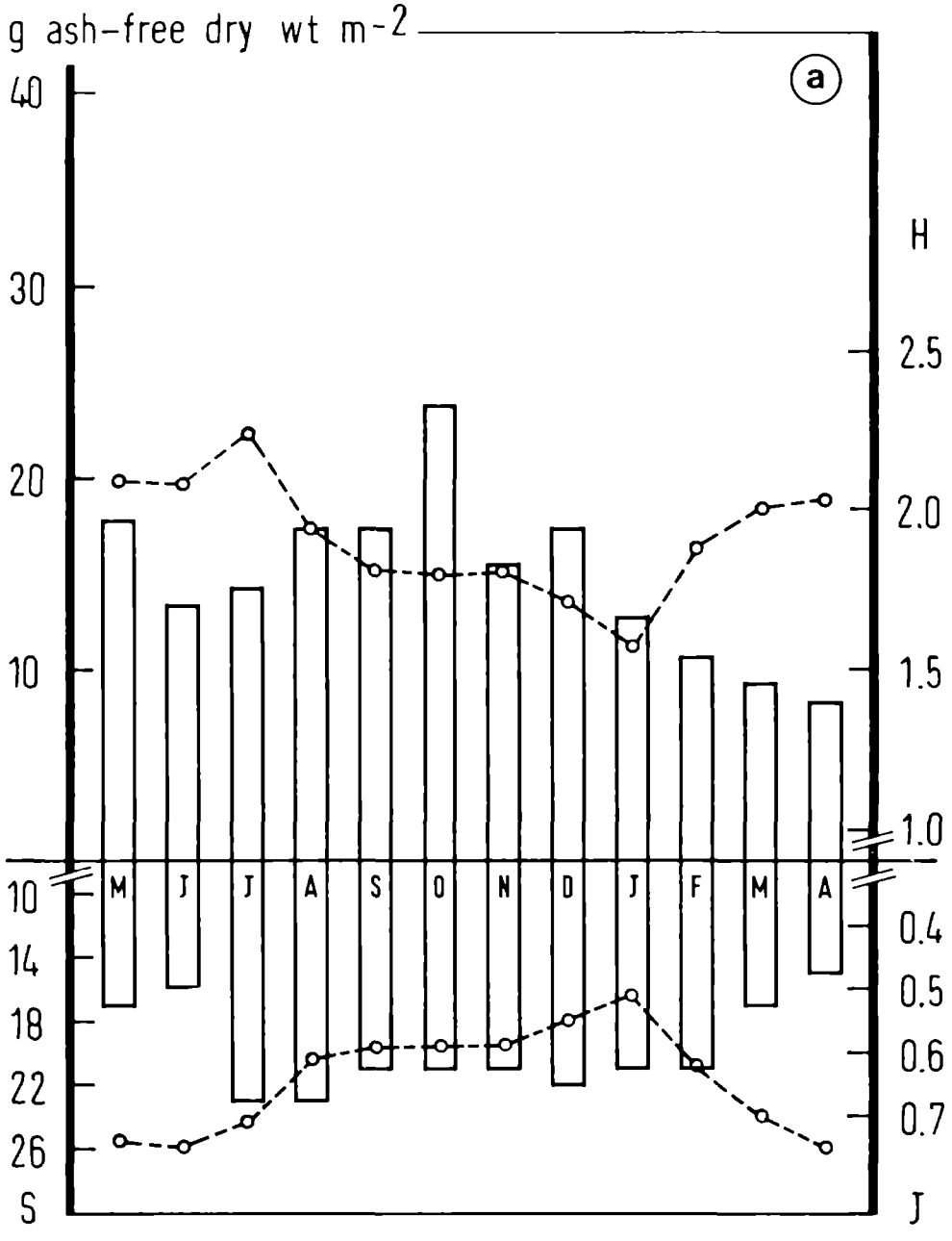

Fig. 7a. See legend on facing page.

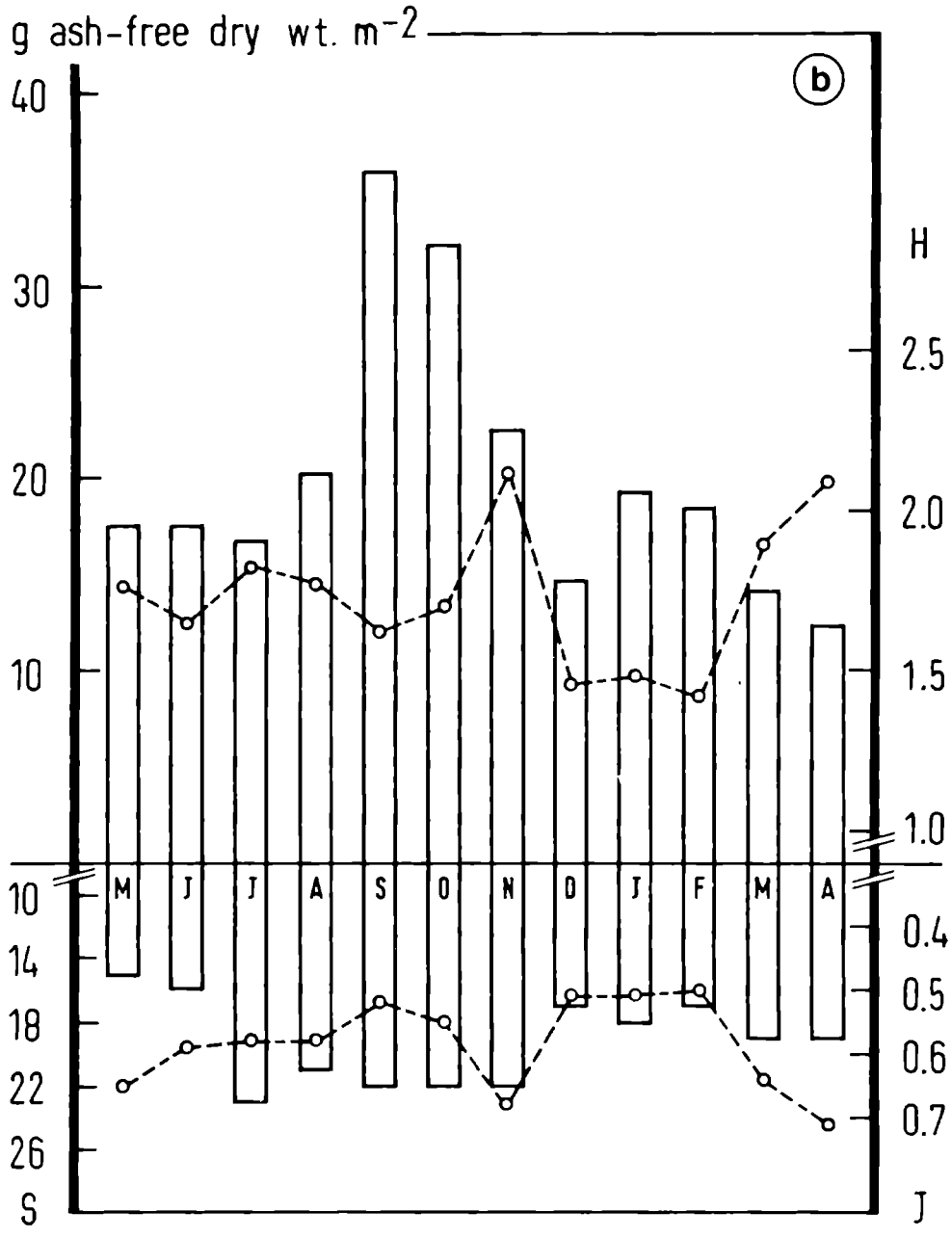

Fig. 7b. Seasonal variations of macrofaunal ash-free dry weights in the samples taken in the high (a) and low (b) littoral Zostera bed in the Krabbenkreek and the relations between species richness and biomass, expressed as diversity (S = number of species; H = diversity index (broken line); J = evenness (broken line)).

density of the species could only be so extremely high because of the actual size of the animals concerned: all species mentioned were relatively small. However, this group of animals showed another similarity: they belonged to the group (1), characteristic for the tidal flats high in the littoral (see p. 130).

Examining the remaining species and especially the species scored in one of both beds for a minimum of 5 months, an overall random distribution was apparent, some of the species showing a tendency to aggregate. This last phenomenon was most conspicuous for the mobile species occurring with high densities in the samples concerned. Lower densities seemed to be a consequence of the ability of and the possibility for individuals to avoid each other. However, the ultimate random distribution pattern could also be due to the influence of one or more environmental factors. At present it seems intractably difficult to differentiate between the relative importance of each factor to the distribution and abundance of the fauna associated with the seagrass. Despite this, a general relationship between occurrence, abundance and random distribution of the fauna, and the presence of seagrass, which also followed a random distribution, seemed to exist. This may explain the distribution patterns of the species for which abundance was correlated to the presence of seagrass.

In addition to the spatial distribution of individuals within a population, it is important to examine the density and the distribution of the populations over the whole seagrass meadow. This is necessary for species showing recognizable differences in abundance between both beds. Most of the species collected appeared to be more or less evenly distributed over the whole Zostera meadow. Major differences were recorded for only a few species and these will be described in detail.

Although the gastropod Littorina littorea is typically an inhabitant of rocky shores, it also occurs on the surface of wet mud and sand (Fretter and Graham, 1980). It was more abundant in the lower bed of the seagrass meadow in the Krabbenkreek (see Table 3). However, the species was present in nearly all samples and appeared to be a common littoral prosobranch. According to Moore (1937) this mainly littoral gastropod did not seem to be bound to a special type of substrate, although on the tidal flats its distribution seems to be governed by the available shelter (Wolff, 1973). This would explain the higher scores in the heavily vegetated lower part of the seagrass bed (compare Table 1 and Fig. 3).

The population density of the polychaete Tharyx marioni in the lower bed was very high compared with that of the higher bed (see Tables 3 and 4). This reflects the preference of the species for mud and muddy sands, as mentioned by Southward (1956, 1957), Gibbs (1969) and Wolff (1973). During the investigation period maximum numbers were found in June (4570 ind.m^{-2}). Ovigerous females were found in June, July and August, after which the population gradually decreased to minimum values of approximately 600 ind.m^{-2} in March 1979. This greatly contrasts with the situation in the higher bed where values reached a maximum of 50 ind.m^{-2}.

The temporarily high numbers of the amphipod Gammarus crinicornis during some of the summer months and especially in the lower bed (see

Tables 3 and 4), seemed to be correlated with the ecological niche preferred by the species. According to Den Hartog (1964) and Vader (1966) this amphipod (sub nom. G. plumicornis) is most abundant between loose-lying algae. In the seagrass meadow this niche was locally present during the summer months (see p. 125).

Abundance patterns reflecting highest scores in the high littoral bed refer to several species i.e. Capitella capitata, Arenicola marina, Retusa obtusa and Corophium volutator. Capitella capitata showed rather fluctuating numbers in the lower bed with an average for the whole investigation period of 113 ind.m^{-2}. In contrast, in the higher bed this value amounted to 760 ind.m^{-2}, with a maximum of 1939 ind.m^{-2} in May 1978. After May the number of specimens slowly and gradually decreased to a minimum of 73 ind.m^{-2} in January 1979, followed by a rapid increase. Apparently the species preferred the more sandy bottom, characteristic for the high littoral bed. This agrees with the observations made by Wolff (1973) and Rasmussen (1973), of which the last author recorded the highest densities in sandy bottoms with a high content of decaying animal and plant debris.

Arenicola marina was found at both sampling stations. Taken as an average over the whole year, densities were observed of 88 and 14 ind.m^{-2} in the higher and lower bed, respectively. These numbers strongly contrasted with countings of faecal heaps, which gave only 30 - 60% of the estimations mentioned above. The lug-worm occurs in a variety of substrates (Muus, 1967). According to Wolff (1973) the only factors which limit the distribution in the Deltaic region are salinity and sediment type. The lower limit of occurrence is an isohaline of 10‰ Cl^-. The apparent preference of A. marina for the lower seagrass bed in the Krabbenkreek, i.e. for a more muddy bottom, supports Longbottom (1970) who showed a correlation between high numbers and the abundance of organic matter in the sediment. Beukema and De Vlas (1979) reported a relationship between abundance and both silt percentage of the sediment and height in the tidal zone, with maximum densities of adults at intermediate levels.

The carnivorous gastropod Retusa obtusa was found with mean numbers of 72 ind.m^{-2} in the higher bed from July 1978 to April 1979 (see Table 3). The highest values were recorded in July, August and September: approximately 200 ind.m^{-2}. In the lower seagrass bed only a few specimens were found. This difference in distribution was marked. Nevertheless an actual relation with a possible causal factor could not be deduced.

Apart from some incidental records in the lower bed, the amphipod Corophium volutator was rather abundant in the higher littoral seagrass bed with an average number of 93 ind.m^{-2} for the whole investigation period. According to Wolff (1973) it occurs mainly in brackish water. It prefers chlorinities ranging from 3 to 12‰ (McLusky, 1970). However, the texture of the bottom also seems to influence the occurrence of the species; Rasmussen (1973) observed that sheltered flats of fine muddy sand form an optimum environment. Reise (1978) regarded the height in the littoral as an important distribution factor and distinguished a C. volutator community close to the high water mark, just above a Zostera noltii meadow. All the mentioned factors may have attributed to the actual distribution and

abundance of the species in the Krabbenkreek. The data given by Reise (1978) seem to contradict the results shown in Table 3, in which C. volutator is seen to be a more or less characteristic inhabitant of the Zostera beds.

DISCUSSION AND CONCLUSIONS

Zostera marina in the Krabbenkreek reflects the characteristics of a typically annual species, i.e. a seasonal regeneration of the vegetation, totally depending on seed production. The seeds germinate in spring with increasing water temperatures. According to Phillips (1971), these conditions seem to be optimal for germination. The rise in water temperature coincides with an increase in insolation (see Fig. 2) and a rapid and prominent increase of the Z. marina cover and biomass (see Table 1 and Fig. 3). This high productivity is associated with the insolation pattern in particular, a relationship also referred to by Sand-Jensen (1975), Jacobs (1979), Wium-Andersen and Borum (1980) and Aioi (1980). The first flowering shoots appear in June and become large structures (see also De Cock, 1980). Apparently all available energy is expended in the production of seeds and the life cycle is completed within a few months. The below-ground biomass is relatively small and in the absence of vegetative expansion the function of the rhizomes seems to be almost completely restricted to anchorage. Hence, the species fails to ensure establishment by asexual reproduction, as shown by the perennial form of Z. marina (Jacobs, 1979, 1982).

The described reproductive strategy of Zostera marina with seasonal regeneration, is apparently related to the suboptimal conditions to which the population is exposed. In such habitats the seagrass is subjected to sub-oceanic salinities (see Fig. 2), which seem to restrict the leaf production in general, and survival of the shoots in winter (Biebl and McRoy, 1971; Pinnerup, 1980). Light and low temperatures in winter can be assigned as another limiting factor at this latitude, particularly during winter. The lower transparancy of the water in the Deltaic region can also be assigned an important factor contributing to limitation of the species.

In contrast, Zostera noltii appears to be a perennial species, of which the production continues all year round, though with lower values during winter. The productivity is characterized by a continuously branching rhizome (see also Tomlinson, 1974) with a production capacity of one leaf at each node. As a consequence the population is independent of the production and germination of seeds. Moreover, these seeds appear to be of minor importance for the propagation of the species: seedlings have been very rarely found. Hence, regeneration occurs by vegetative expansion of the rhizome fragments, which have overwintered. However, in this habitat the vegetation is subjected to a predictable seasonal damage by grazing waterfowl (Wolff et al., 1967; Wolff et al., 1976; Wolff and Post, 1979). This situation is comparable with the Dutch Wadden Sea, where approximately 50% of the maximum seagrass standing stock was lost by grazing (Jacobs et al., 1981). In the Deltaic region the bird species

using Zostera as a food source are the same as in the Wadden Sea, i.e. the brent goose (Branta bernicla (L.)), the pintail (Anas acuta L.), the wigeon (Anas penelope L.) and the mallard (Anas platyrhynchos L.). In 1967 Wolff et al. reported a remarkable correlation between the distribution of the Zostera species and that of brent geese. The favourite food plants for these birds seem to be seagrasses as well as green algae, Enteromorpha spp. and Ulva spp. (Ranwell and Downing, 1959; Burton, 1961, 1962; Wolff et al., 1967; Charman, 1979). These birds have also been observed in the Krabbenkreek, but we were not able to qualify and quantify their consumption. However, the effects of "grazing" (Jacobs et al., 1981) are most striking, as since the arrival of birds (the first considerable numbers were observed in October and November) the amount of seagrass decreased very quickly (see Table 1 and Fig. 3). By the end of the year the cover had declined to almost zero, however part of the below-ground biomass was still present (Fig. 3). Comparing the data given in Table 1, the two seagrass beds seem to be unequally grazed, as the higher precentage cover in the lower bed decreased relatively faster than in the higher bed, apparently due to a difference in grazing pressure. The birds appear to prefer to feed in the most dense vegetation. This has also been reported by Jacobs et al. (1981) in a detailed study of grazing of seagrass by birds in the Dutch Wadden Sea.

Reviewing the knowledge of animal communities associated with seagrass beds on a world wide basis, Kikuchi and Pérès (1977) and Kikuchi (1980) suggested a remarkable degree of parallelism in both structure and function. Structure of the animal communities is related to a differentiation of the plant community into a number of vertically arranged 'frame-elements' (e.g. leaves, stems, etc.), which increase the diversity of habitats available for animals. In an attempt to summarize the structural composition of seagrass communities Den Hartog (1979) distinguished 9 components related to animal species within a total of 19 elements. The presence and diversity of the faunal components are locally determined by the identity and the characteristics of the plant species and by the abiotic environment. The structure of the seagrass bed in the Krabbenkreek was completely determined by the physico-chemical environment characteristic for the intertidal muddy substrate of the estuary. General information about the hydrography and topography of the Delta and the inhabiting soft-bottom macrofauna was given by Peelen (1970) and Wolff (1973). The hydrographical characteristics of this area result in annual fluctuations of temperature and salinity in the Krabbenkreek (see Fig. 2). In addition, in the littoral yearly and diurnal changes enlarge the amplitude of these fluctuations, which probably determine the extent of penetration of the typically marine phanerogam Zostera marina in this estuary. Phenological and physiological adaptation of the species to this environment results in the life-strategy observed and also manifests itself in a reduction in number of the frame-elements of the plant community, both in a spatial and temporal sense. In the Krabbenkreek, therefore, Z. marina seems to occur at the extreme limit of its distribution area. Moreover, as a consequence of grazing by birds, above-ground plant parts are only temporarily present. Thus, in addition to a limited number of

frame-elements of the plant community, the presence of this frame and/or its particular elements varies considerably on a yearly basis.

The general consistency of the above described factors determines the ultimate presence and abundance of the macrofaunal species recorded. For many species, including stenotherm and fresh-water species (e.g. Chironomus sp.), the higher parts of the estuarine tidal area form an important biological limitation to their occurrence. Wolff (1973) considered the true euryhaline species generally found in brackish water to be typical inhabitants of muddy sediments. The species listed by this author as common for the tidal flats of the Oosterschelde also appear to be dominant in the Krabbenkreek. Wolff (1973) recorded a maximum of 23 species in this area and from his rarefaction curves, a diversity can be deduced ranging from 17 to 22 species per 200 individuals. However during that study, in 1962, the Krabbenkreek was both on the east and west side in open connection with the Oosterschelde, and consequently characterized by a stable high salinity. In our study a less diverse fauna was found with 11 to 17 species per 200 individuals, probably due to changed hydrographical conditions since 1962. On the contrary, the maximum number of taxa collected with all the samples in 1978/1979 amounted to 35. This conspicuous difference may be ascribed to the intensive and adequate sampling procedure applied in this study and to the special habitat created by the presence of seagrass. Apparently a functional relationship exists between the inhabiting fauna and the vegetation, resulting in higher values of species occurrence and abundance.

Several functional aspects of seagrass in relation to the faunal components have been mentioned by Den Hartog (1977) and Kikuchi (1980). Direct trophic relationships are mainly restricted to tropical and subtropical areas (see McRoy and Helfferich, 1980). In temperate regions only a few invertebrates feed on living seagrass (see Nienhuis and Van Ierland, 1978), in addition to temporary and locally intensive grazing by waterfowl (Martin et al., 1951; Jacobs et al., 1981), which was also reported in this study. This may indicate that the macrofauna, associated with the seagrass in the Krabbenkreek, used the bed mainly as a shelter, a spawning site or food source, with the restriction that they preferred other food to seagrass.

The quantitative analysis of the macrofauna resulted in 3 groups of species, of which the group characteristic for the tidal flats was most abundant. As a consequence of the minor numerical importance of the group associated with the vegetation (Table 3), the whole assemblage is only slightly different from the surrounding unvegetated areas. The species abundance and diversity in the community is thus determined by the rather unstable environment in the tidal region. The degree of dominance or the complexity of the faunal assemblage is only comparable with other eelgrass communities by using the H-index as an objective numerical tool. The calculated diversity indices based on numbers ranged from 1.07 to 1.98. These values were higher than in plant communities under brackish conditions (see Lappalainen and Kangas (1975) for Zostera marina and Verhoeven (1980) for Ruppia spp.), whereas the mean total numbers of individuals reported from those habitats were smaller than those found in the Krabbenkreek. Comparison with data from subtidal localities, given by O'Conner

(1972), Marsh (1973) and Orth (1973), showed a lower species diversity in this study. Considering the diversity for some structurally different seagrass communities near Roscoff, France (Jacobs and Huismann, 1982), the values for the Zostera noltii stands in the higher parts of the littoral (ranging from 0.73 to 2.09) were of the same magnitude as those in the Krabbenkreek. In general, the diversity values for the Zostera marina stands at Roscoff appeared to be higher. Due to the comparable environmental conditions, the two Z. noltii communities probably had a corresponding structure and complexity.

Despite the numerical dominance of smaller worms, the biomass was mainly determined by the molluscs. The average values of 14.8 and 20.1 ash-free dry wt m^{-2} for the higher and lower bed, respectively, agreed very well with data from Zostera marina stands in Tvärminne (Finland). There Lappalainen et al. (1977) measured an average faunal biomass of 17.3 g ash-free dry wt m^{-2} with a dominance of molluscs. O'Connor (1972) reported very low values in Zostera stands (0.7 - 6.1 g ash-free dry wt m^{-2}) from Moriches Bay, New York.

Considering the niche differentiation of the species found in the Deltaic region, Wolff (1973) concluded that the shores of the Oosterschelde harboured the most diversified fauna with representatives of all feeding types. The feeding type of the dominant species found in the present study is given in Table 4. Examination of the numerically dominant species, shows an overwhelming component of deposit feeders, whereas in terms of ash-free dry weight the fauna was more obviously represented by all trophic levels. Apparently many niches and micro-habitats in the seagrass community are occupied. However, a direct relationship between the seagrass plants and the inhabiting fauna could not be demonstrated.

In an attempt to classify Zostera biocoenoses with respect to their composition of flora and fauna, Jacobs and Huisman (1982) proposed that floristic, structural and ecological criteria have to be used to indicate the number and characteristics of the micro-habitats available. In practice they distinguished six structural characteristics for a qualification, and on the basis of their investigation near Roscoff (France) they arrived at the following three units:

1 Biocoenoses of Zostera noltii stands under eulittoral conditions on muddy bottoms.
Simply structured communities with a dense benthic fauna, of which the majority belong to the selective deposit-feeders.

2 Biocoenoses of Zostera noltii stands under eulittoral conditions on sandy bottoms.
Simply structured communities with a dense benthic fauna, of which the majority belong to the non-selective deposit-feeders.

3 Biocoenoses of perennial Zostera marina stands under both eulittoral and submerged conditions, forming a continuum.
Sub-biocoenoses can be distinguished by qualification and quantification of the structural elements in the vegetation.

Examination of all structural characteristics of the seagrass community described in this study and especially the pure Z. noltii stands in the upper part of the meadow, show a particularly close resemblance to the above given second biocoenose. Gradually more Z. marina was recorded towards the lower parts, mostly growing in slight depressions and covered with some water. In an attempt to classify the seagrass communities in a hierarchic, phytosociological system, Harmsen (1936) distinguished the associations Zosteretum marinae stenophyllae and Zosteretum nanae (Z. noltii) in the littoral. These associations showed intermediate forms by the occurrence of mixed stands of Z. noltii and the smaller Z. marina (as Z. marina var. stenophylla Aschers. & Graebn.). Comparable stands were reported in the Dutch Wadden Sea by Den Hartog and Van der Velde (1970) and Polderman and Den Hartog (1975), and in this study in the Krabbenkreek. It seems justified to consider these communities variants of the second biocoenose described by Jacobs and Huisman (1982) and to refine the description as "biocoenoses of Zostera noltii stands sometimes mixed with annual Z. marina, under eulittoral conditions on sandy bottoms".

ACKNOWLEDGEMENTS

We wish to thank Professor Dr. C. den Hartog, Dr. W.J. Wolff and Dr. J.T.A. Verhoeven for reviewing the manuscript. Dr. Connie A.N. van Oorschot corrected the English text. We are also indebted to Dr. C. Erséus (Gothenburg) for the identification of some Oligochaeta, Mr. W. Lemmens for help with the computations, Mr. J.J.A. Slippens for the drawings, Dora Williams for typing the manuscript and Mr. J. Pieters (Rijkswaterstaat, Middelburg) for the environmental data. The data and the map on the distribution of seagrass in the Oosterschelde were provided by Eugène Daemen. Finally a special word of thanks to the farmer Mr. P. Polderman for kindly using his tractor when our vehicle was lodged in the mud.
This project has been financed by the Netherlands Organization for the Advancement of Pure Scientific Research (ZWO).

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Aquatic Botany, 10 (1981) 241—259
Elsevier Scientific Publishing Company, Amsterdam — Printed in The Netherlands

GRAZING OF THE SEAGRASS *ZOSTERA NOLTII* BY BIRDS AT TERSCHELLING (DUTCH WADDEN SEA)

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(Accepted 22 August 1980)

ABSTRACT

Jacobs, R.P.W.M., den Hartog, C., Braster, B.F. and Carrière, F.C., 1981. Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). *Aquat. Bot.*, 10: 241—259.

On the tidal flats south of the island of Terschelling in the Dutch Wadden Sea a seagrass bed is situated, which covered an area of 107 ha in 1974. The dominant species in this bed was *Zostera noltii* Hornem., but scattered single shoots of *Zostera marina* L. also occurred. Maximum standing stock estimations for the whole bed amounted to 2778 kg dry wt. in 1974.

The island of Terschelling is an important roosting place for wildfowl in the Dutch Wadden Sea. Four species, viz. the brent goose (*Branta bernicla* (L.)), the pintail (*Anas acuta* L.), the wigeon (*Anas penelope* L.) and the mallard (*Anas platyrhynchos* L.) use the intertidal *Zostera noltii* as a food source.

Censuses taken during the autumn of 1974 showed that an average of 710 birds remained on the seagrass vegetation each day. From 10 September to 8 December these birds consumed 1426 kg dry wt. of seagrass, *Anas acuta* and *Anas penelope* taking the greatest share of 66%. Since the winter standing stock was very low, ca. 1300 kg dry wt., i.e. approximately 50% of the total amount must have been lost due to dying off, consumption by invertebrates and breaking off by wave action. This figure agreed with estimates of the biomass decrease in two enclosures.

A detailed study of the effect of grazing on the seagrass vegetation showed that the initial cover of the seagrass determined the whole grazing process, the birds preferring to feed in the most dense and homogeneous beds. Intensive grazing initially caused an increase of the heterogeneity but ultimately resulted in a homogeneous vegetation with a very low percentage cover, that is to say an almost total disappearance of the above-ground parts of the plant.

INTRODUCTION

Two seagrass species occur in The Netherlands, *Zostera marina* L. (eelgrass) and *Zostera noltii* Hornem. During recent decades the extent of the seagrass

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populations has changed considerably. After the 'wasting disease' in the 1930s, no recovery of the sublittoral *Z. marina* beds in the Dutch Wadden Sea has taken place. During the last 10 years the eulittoral populations of *Z. marina* have almost disappeared and those of *Z. noltii* have shown a slow, but general decline (den Hartog and van der Velde, 1970; den Hartog and Polderman 1975; Polderman and den Hartog, 1975; van den Hoek et al., 1979). In the Delta region in the SW. Netherlands both species occur only on the tidal flats, but since the closure of the Grevelingen estuary in 1971 the *Z. marina* beds have undergone rigorous expansion in the brackish Lake Grevelingen (Nienhuis and de Bree, 1977).

The importance of the *Zostera* communities in coastal waters is recognised (den Hartog, 1977), the most prominent function of these communities being their high production rate, in the range of 0.2—7.0 g C m^{-2} day^{-1} (McRoy and McMillan, 1977). However, most organic material produced by the seagrasses only becomes available via decomposer food-chains, as very few animals are able to utilise seagrass tissue directly (Fenchel, 1977). In northern temperate areas, these species are predominantly herbivorous birds (Ranwell and Downing, 1959; Charman, 1977, 1979) and some invertebrates (Nienhuis and van Ierland, 1978; Nelson, 1979).

Seagrasses, when present, form an important food source for brent geese, *Branta bernicla* (L.), and wigeon, *Anas penelope* L. (Campbell, 1946; Burton, 1961, 1962; Maheo, 1976; Wyer et al., 1977; Charman and Macey, 1978; Charman, 1979). It is generally assumed that the grazing of seagrasses by birds plays a minor role compared with the decomposition of tissues by micro-organisms (Mann, 1972; Kikuchi and Pérès, 1977). Data from the submerged eelgrass beds in Lake Grevelingen (SW. Netherlands) supported this belief (Wolff et al., 1976; Nienhuis and van Ierland, 1978).

The purpose of this study was to evaluate the most important factors generating the observed changes in pattern of the *Zostera noltii* vegetation. An attempt was made (1) to quantify the seagrass consumption by birds on tidal flats which were easily accessible to them and (2) to examine the effects of grazing on the vegetation and structure of the seagrass bed.

THE STUDY AREA

South of the island of Terschelling on the tidal flats near Oosterend, a bed of *Zostera noltii* is situated. The position of this bed in 1974 was approximately the same as in 1973 (see Polderman and den Hartog, 1975), although the total area covered by seagrass had decreased from 154 ha in 1973 to 107 ha in 1974. In this bed, *Z. noltii* occurred on the gently sloping elevations of the flats. These small hillocks originated from sediments and other substances transported by tidal currents; the seagrass shoots encouraged sedimentation and helped to prevent erosion. In the shallow depressions where water was retained at low tide, a few scattered *Z. marina* shoots were found. In 1973 it was possible to describe the area covered with *Z. marina* in terms of cover percent-

ages and so the situation in 1974 represented a considerable decrease in the standing crop of this species.

Zostera marina apparently did not overwinter, and the distribution of these eelgrass shoots appeared totally dependent on annual seed production. In spring seeds germinated, and during the growing season the shoots expended the greatest part of their energy on sexual reproduction and consequently had an underdeveloped rhizome. This phenomenon has also been described by Keddy and Patriquin (1978) for eelgrass in Nova Scotia (Canada) and by Bayer (1979) for eelgrass in the Yaquina estuary (Oregon). In autumn the *Z. marina* shoots died back completely, as distinct from the eelgrass populations along the Brittany coast where both above-ground and below-ground production continued during the winter (Jacobs, 1979). In contrast both above-ground and below-ground production of *Z. noltii* continued throughout the year, with maximum values from June to November, resulting in luxuriant vegetation during these months. During autumn and winter, the biomass of this seagrass decreased, due not only to a decrease in production rate and damage by water movement, but also because of the grazing by birds.

Terschelling is one of the most important resting areas for wildfowl in the Wadden Sea during their migrations to and from their arctic breeding grounds in Scandinavia and Russia (Mörzer Bruyns and Timmerman, 1968; Mulder, 1977). The area is used primarily as a wintering area but secondarily as a migration stop. The number of species which use *Zostera* as a food source is limited to four: the brent goose (*Branta bernicla* (L.)), the pintail (*Anas acuta* L.), the wigeon (*Anas penelope* L.) and the mallard (*Anas platyrhynchos* L.).

MATERIAL AND METHODS

In July and August 1974 the seagrass bed was mapped. Twelve 5-m wide transects perpendicular to the coastline were plotted, and in these areas the seagrass was quantified by counting the number of shoots and by estimating the percentage leaf cover. The biomass was determined by taking 20 × 20 cm samples from stations with different densities, and drying these for 24 h at 95° C. The percentage cover, the number of shoots in the samples and the biomass were correlated. The pattern of vegetation was studied by comparing the quantities of seagrass within adjacent parts of the transects. Points with equal densities were joined, resulting in series of lines or isopleths. From the isopleth map the total area and the total standing crop was calculated.

From 10 September to 9 December 1974 during almost every low water period (except those at night) the number of birds feeding on seagrass was counted (60 times in total). Several censuses throughout one low-water period indicated the likely temporal variability of these figures. Censuses and observations on the feeding behaviour of the different bird species were made from a hut (see Fig. 1) placed at the approximate centre of the bed. To obtain the number of bird days the number of birds present at the seagrass bed during each low-water period was multiplied by the length of the matching low-water

Fig. 1. The observation post in the *Zostera noltii* bed on the tidal flats near Terschelling.

period. The standard metabolism (SM) of the birds (kcal day^{-1}) was calculated using the relation given by Lasiewski and Dawson (1967)

$$\log SM = \log 78.3 + 0.723 \log W$$

where W is the body weight in kg (values were taken from Bauer and Glutz von Blotzheim, 1968). To obtain the consumption per bird per day the standard metabolism was multiplied by a factor of 3 for net food assimilation and by a factor of 1.67 for food assimilation efficiency (see Lambeck, 1973; Nienhuis and van Ierland, 1978). Values in kJ were converted to g dry wt. by multiplication by 0.2 (Winberg, 1971).

A more detailed study of the mechanism and the effect of grazing was carried out from 11 October to 3 December 1974 within four 50 × 20 m plots, situated to the north, east, south and west of the observation post. Within the plots the cover of *Zostera noltii* was estimated for each m^2 on a five point scale: (0) < 4 shoots; (1) from 4 shoots to a cover < 10%; (2) cover 10—25%; (3) cover 25—50%; (4) cover 50—100%. The heterogeneity (H) of the vegetation was estimated using the formula

$$H = \sum |C_x - C_y|$$

where C_x is the cover value of the x^{th} plot ($1 m^2$) and C_y is the cover value of each plot ($1 m^2$), surrounding the x^{th} plot. Consequently, the heterogeneity value per m^2 ranged theoretically from 0 (maximum homogeneity) to 32 (maximum heterogeneity). To obtain the heterogeneity index, the value of H was expressed as the percentage of the theoretical maximum for the whole plot, i.e. 16 on average.

Ungrazed vegetation was studied in two 6 × 6 m enclosures. These areas were covered with a net at a height of 50 cm above the vegetation, which hung down at the sides as far as the mud surface.

RESULTS

Birds grazing on the Zostera noltii *bed and their seagrass consumption*

During low-water periods, several bird species regularly foraged over the seagrass bed on the tidal flats: oyster-catchers, curlews, shelducks and gulls were always present, and in the late summer dunlin, knot, redshank, greenshank and sometimes grey plover were also present. These species searched for animal food in the mud or between the seagrass shoots. From September to 9 December the four seagrass-consuming bird species (Fig. 2) were studied. The wigeon (*Anas penelope*) and mallard (*Anas platyrhynchos*) were present on the first day of the observation period (10 September). The first specimens of the brent goose (*Branta bernicla*) arrived on 22 September, and those of the pintail (*Anas acuta*) on 10 October. Table I summarizes the numbers of these four bird species observed on the seagrass bed during the entire observation period. The numbers were derived from almost daily observations. However, the accuracy of the counts was variable and depended mainly on the weather conditions. The possible degree of variation of the census figures for the different species amounted to 8%, 16%, 19% and 28% for brent goose, pintail, wigeon and mallard, respectively.

The maximum numbers of birds on Terschelling (obtained from censuses on saltings and inland meadows during the high water periods) can be compared with the daily mean on the *Zostera* bed (see Table I). Only for pintail did the seagrass appear to be of direct importance as a daytime food source.

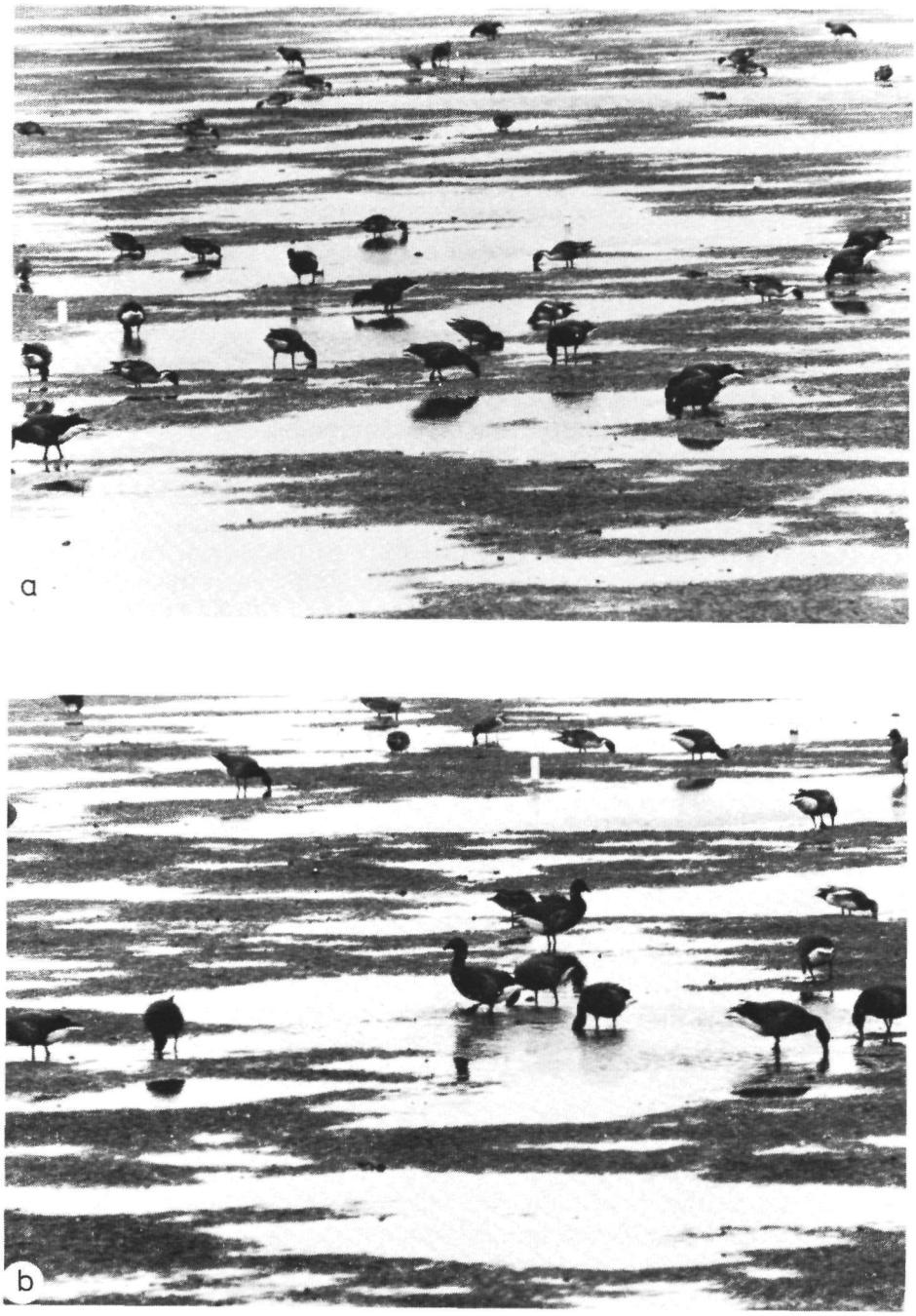

Fig. 2a. Brent geese, pintail and mallard grazing on the *Zostera noltii* bed south of Terschelling in the Dutch Wadden Sea. (b) Brent geese, pintail and mallard on the *Zostera noltii* bed. Note the goose 'trampling' in the centre of the picture.

TABLE I

Numbers of herbivorous birds observed during the autumn of 1974 (10 September—8 December) on the *Zostera noltii* bed south of the island Terschelling in the Dutch Wadden Sea, and their percentage in relation to the maximum numbers of the wintering population on Terschelling

Species	World population	Numbers on Terschelling				
		Maximum numbers in autumn and winter	Numbers on *Zostera* bed			
			Daily mean	(%)	Maximum	(%)
Branta bernicla	71 000*	16 000	209	1.3	339	2.1
Anas acuta	70 000**	750	260	34.7	732	97.6
Anas penelope	500 000**	22 000	185	0.8	1292	5.9
Anas platyrhynchos	1 500 000**	1600	56	3.5	112	7.0

*International Waterfowl Research Bureau (IWRB).
**Atkinson-Willes (1972) and Szijj (1972).

An average of almost 35% of the population at Terschelling stayed on the bed during the day.

The biological importance of Terschelling as one of the wintering sites for waterfowl in western Europe is demonstrated by the presence of 40 350 geese and ducks in the winter (see Table I). The international importance of the area for the brent goose is shown by the 23% of the world population which stayed on the island.

During the daytime low-water periods the activity of the seagrass consuming birds on the bed was observed. The birds flew about for a period of 30—60 min between their high-water grounds to the seagrass bed as the water level fell. They then swam until their food became accessible. Foraging for food continued throughout the low-water period, which lasted 5 h 11 min on average. The birds left the feeding grounds together as soon as the water rose just above the vegetation. The numbers of birds varied greatly from day to day during different low-water periods, and even during one low water cycle, because of disturbance. The numbers of bird days of each species have been calculated for the whole observation period from the mean numbers present during each low water period and the lengths of these periods (see Table II). Using these data and figures for standard metabolism, the total amount of seagrass consumed was calculated as 1426 kg dry wt., of which *Anas acuta* and *Anas penelope* took the greatest share of 66% (Table II).

The determination of the total standing crop was carried out in July and August (the months with maximum biomass), using the isopleth map. Within every isopleth the average number of shoots m^{-2} and the standing crop was determined. There appeared to be a significant linear relationship ($P < 0.001$) between these two parameters: $y = 0.050\,x + 4.972$ ($r = 0.97$), where y is the

TABLE II

Zostera noltii consumption by birds on 10 September—8 December 1974 on the tidal flats at Terschelling

Species	Birds		Bird days	Seagrass consumed		
	Weight* (kg)	Standard metabolism** (kJ day^{-1})		kJ (× 10^6)	kg dry wt.	(%)
Branta bernicla	1.4	419	2717	5.7	272	19
Anas acuta	0.8	281	6604	9.3	444	31
Anas penelope	0.6	226	9188	10.4	497	35
Anas platyrhynchos	1.1	352	2533	4.5	213	15
Totals			21 042	29.9	1426	100

*Bauer and Glutz von Blotzheim (1968).
**Lasiewski and Dawson (1967).

standing crop (g dry wt. m^{-2}) and x is the number of shoots m^{-2}. Using the total areas within the isopleths, the standing crop of the whole *Zostera noltii* bed (107 ha) was calculated as 2778 kg dry wt.

In order to arrive at an estimate of the total annual production, the value of the maximum standing stock was doubled (see Petersen, 1913; Mann, 1972). Although such a calculation gives an underestimate of production for *Zostera marina* (Sand-Jensen, 1975; Jacobs, 1979), the doubling of the maximum standing stock gives a good estimate of the annual production for *Z. noltii*, because of its very low production values during the winter period. Total production for the whole bed amounts to 5556 kg dry wt. The calculated consumption of 1426 kg dry wt. by the geese and ducks (see Table II) therefore approximates to 50% of the maximum standing stock or 26% of the annual production.

Feeding behaviour

The birds arrived in the vicinity of the seagrass bed approximately 50 min before the bed became completely exposed and they swam until their food could be reached. The numbers of birds on the bed during daylight low-water periods and during twilight periods at sunrise and sunset were compared statistically. It appeared that the numbers present at the seagrass bed were correlated with time of low water for three species, but not for the wigeon. When low water coincided with sunrise or sunset, the geese began feeding at first light and in the evening they left when darkness fell, a phenomenon also observed by Maheo (1976). However, the other species could be heard during the nightly low-water periods. The numbers of pintail and mallard present on the seagrass bed were greater during earlier and later low-water periods than in the periods in full daylight.

The observed grazing rhythm agrees with the ecological divergence manifesting itself in the grazing behaviour of the four species: the geese can be regarded as sight-feeders, mallard and pintail as touch-feeders and wigeon as non-specific.

The methods used by the four species whilst feeding on seagrass can be divided into five categories (Table III), of which four were employed during the low water period:

(1) Pecking. Only geese and wigeon pecked at leaves and consumed them (sometimes together with some rhizomes). The preference for the above-ground plant parts has also been reported by Campbell (1946). The birds looked mainly for seagrass vegetation with a relatively high density, situated in small depressions with some standing water, so that the leaves floated on the water surface and could be easily pecked.

(2) Trampling. This type of behaviour was occasionally observed in the geese. Here, whole plants were removed, leaving holes of ca. 20 cm in diameter. Burton (1961) and Fog (1967) also reported the trampling by the geese.

(3) Grubbing. All four species grubbed purposefully with their beaks for whole plants, leaving small holes of ca. 10 cm in diameter and ca. 5 cm deep.

(4) Digging. This type of feeding behaviour was used by all species except the goose, resulting in holes of 20—50 cm in diameter (Fig. 3a). This behaviour also occurred at places without any visible above-ground seagrass cover. Birds were apparently searching for rhizomes.

(5) Swimming. During rising and receding tides, while some water was above the seagrass bed all four species swam and tore up leaves or whole plants with their beaks.

The gaps and depressions in the seagrass vegetation originating from the grazing activities of the birds were in part removed and levelled by the flood current of the next tidal cycle (Fig. 3b).

TABLE III

Feeding behaviour of birds on the *Zostera noltii* bed (+++ most frequently explored; ++ frequently; + seldom observed and then only under very specific conditions (see text); — never observed)

Species	Pecking	Trampling	Grubbing	Digging	Swimming
Branta bernicla	+++	+	++	—	+
Anas acuta	—	—	++	++	+
Anas penelope	++	—	+	++	+
Anas platyrhynchos	—	—	+	+++	+

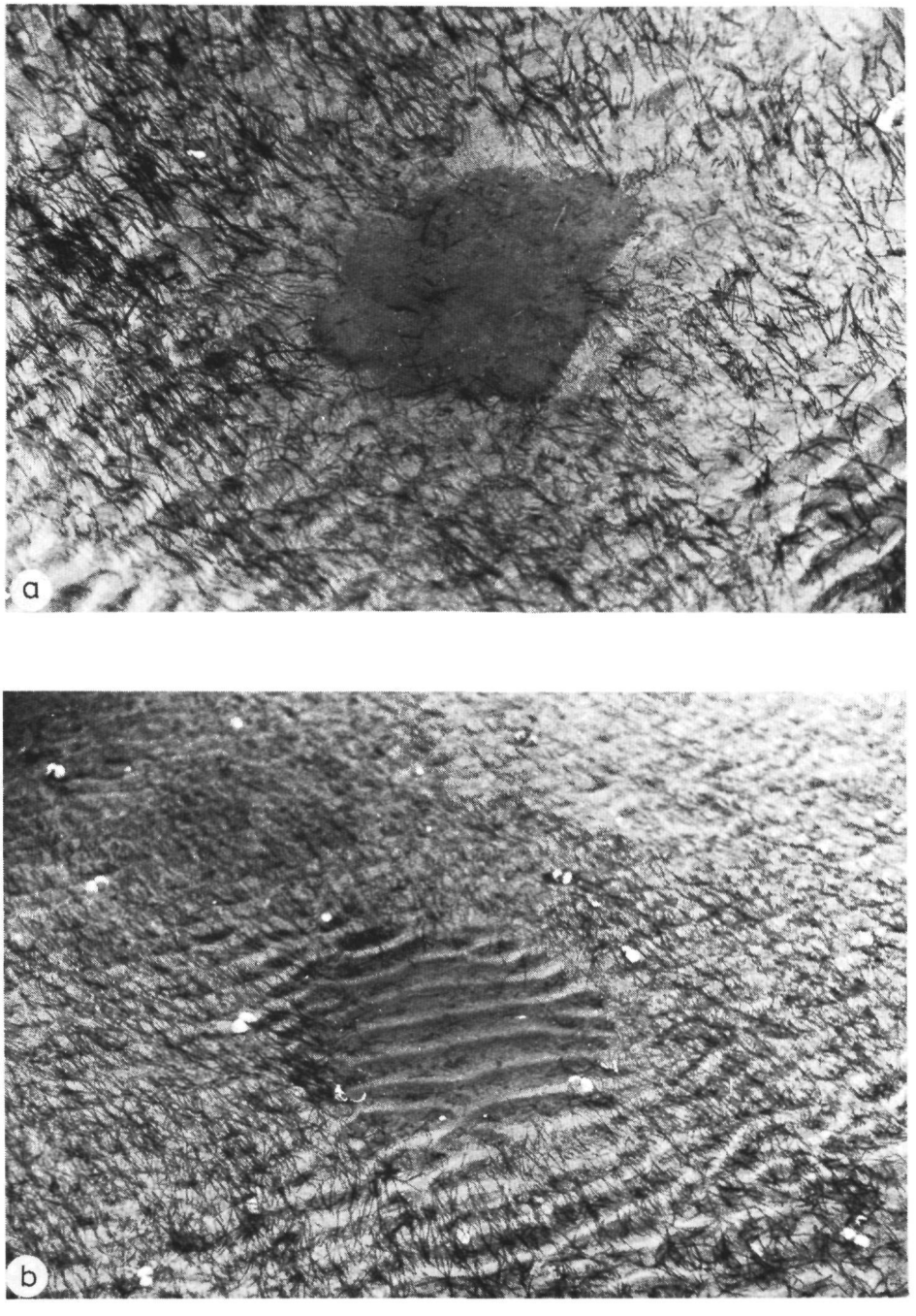

Fig. 3. Holes in the *Zostera noltii* bed: (a) left by digging birds; (b) caused by grazing, and levelled during the following high tide.

Effect of grazing on seagrass in permanent plots

The birds grazing in the four permanent 1000 m^2 plots were observed intensively from 11 October to 3 November. During the low-water periods, the numbers of each species were counted and the duration of their stay in each plot was noted; this was accomplished by making observations every 4 min. The resulting bird days are summarized for each species in Table IV. It appears that the geese spent the greatest time on the seagrass bed, 60.6% of the total number of bird days. The consumption of seagrass calculated for this period was 3.03 kg dry wt.; 69.3% of this was eaten by the geese (see Table IV). However, Table II shows that, for the whole observation period (10 September—9 December), the emphasis was different, geese taking only 19% and the ducks 81% of the total consumed. The differences were a result of the large number of geese in October whilst pintail and wigeon reached a maximum in November. The calculations of the amounts of seagrass taken from the four plots (Table IV) are not comparable between species, because of the unequal numbers of the different species. Therefore, the amounts are of a relative value, applying only to the period indicated, and are not comparable with the data for the autumn as a whole (see Table II).

The consumption of seagrass by the birds did not occur uniformly over the bed (see Table IV). All species preferred to graze in the northern and western plots and took almost 91% of the total amount of seagrass consumed during the period in that area.

The effects of grazing on the seagrass vegetation have been studied by mapping the four permanent plots at three different times in the period 30 September—30 November (Table V). The mappings consisted of determinations of the percentage, cover of every square meter within each plot. The data for the northern plot are given as an example in Fig. 4. The overall decrease of the cover with time coincided with an increase of the homogeneity as indicated by the increase in frequency of a distinct cover value.

The average percentage cover of all plots for the months of October and November are given in Table V and Fig. 5. The calculated heterogeneity indices are also given in Table V. It appears from these data that the whole grazing process was determined by the initial cover: the final cover values were inversely proportional to the initial values. In addition, the grazing pressure of the sight-feeders (geese and wigeon) was proportional to the initial cover values (see Tables IV and V). It can be concluded that the birds preferred to feed in the most dense vegetation, i.e. in the northern and western plots. This conclusion can also be deduced from the censuses described above. The preference for high cover of seagrass can also be deduced from a comparison of the sequence of cover and heterogeneity with time (Table V). The final heterogeneity indices were proportional to the final cover values and the greatest intermediate index occurred in the plot with the highest initial cover (the northern plot). The birds apparently searched the vegetation with the highest cover and under influence of grazing the heterogeneity index initially in-

TABLE IV

Zostera noltii consumption by birds in four 1000 m² plots (N, E, S, W) at Terschelling in the period 11 October—3 November 1974

Species	Birds		Bird days					Seagrass consumed						
	Weight* (kg)	Standard metabolism** (kJ day^{-1})	N	E	S	W	Total	kJ (× 10⁴)					kg. dry wt.	(%)
								N	E	S	W	Total		
Branta bernicla	1.4	419	10.14	1.47	0.10	9.25	20.96	2.13	0.31	0.02	1.94	4.40	2.10	69.3
Anas acuta	0.8	281	2.19	1.35	0.04	5.70	9.28	0.31	0.19	0.01	0.80	1.31	0.63	20.8
Anas penelope	0.6	226	1.07	0.33	0.00	0.81	2.21	0.12	0.04	0.00	0.09	0.25	0.12	4.0
Anas platyrhynchos	1.1	352	0.33	0.12	0.00	1.66	2.11	0.06	0.02	0.00	0.29	0.37	0.18	5.9
Totals			13.73	3.27	0.14	17.42	34.56	2.62	0.56	0.03	3.12	6.33	3.03	100.0

*Bauer and Glutz von Blotzheim (1968).
**Lasiewski and Dawson (1967).

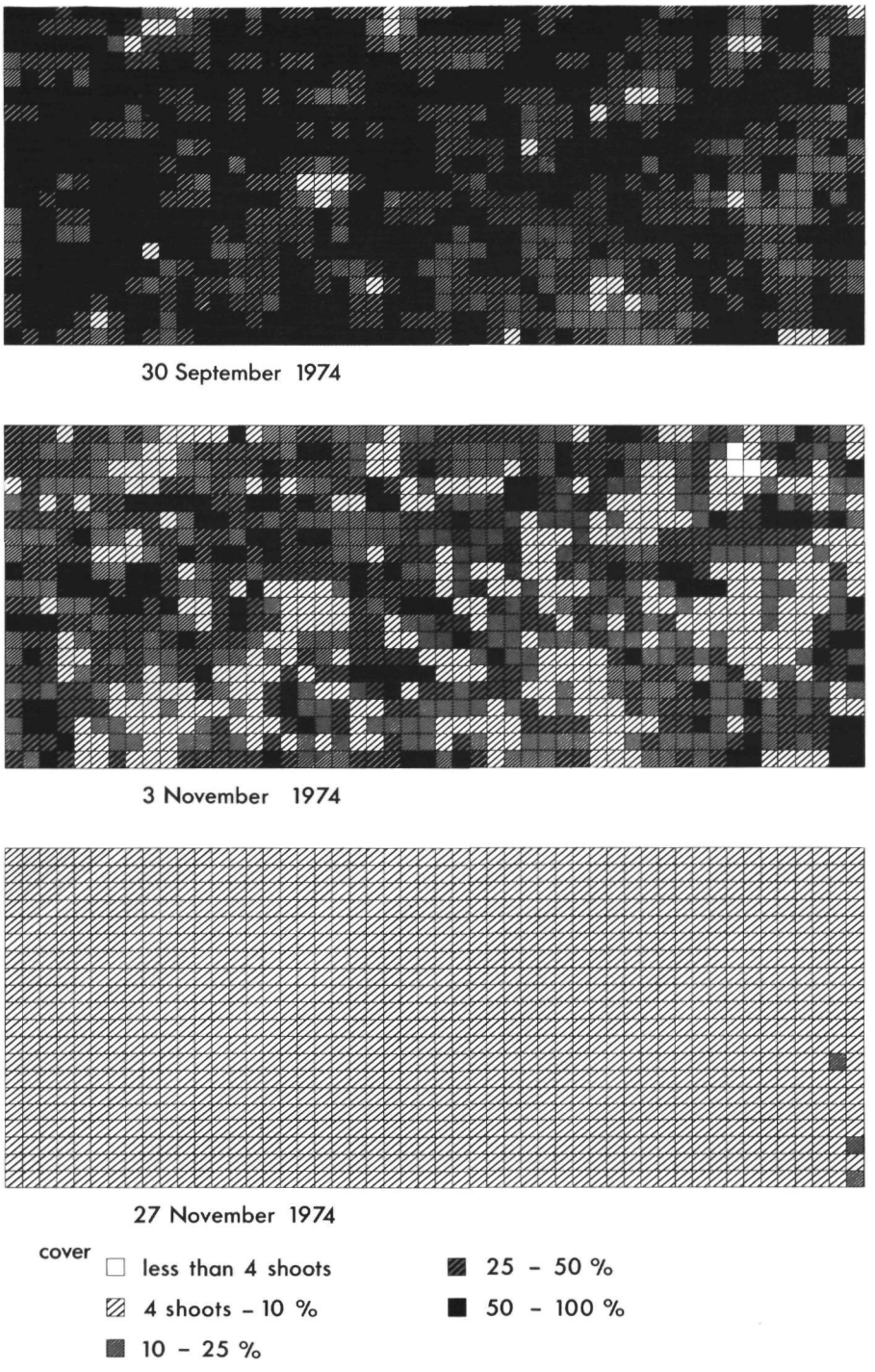

Fig. 4. The effect of grazing on the cover of *Zostera noltii* in the northern 1000-m² permanent plot. Note the increased heterogeneity of the vegetation on the second date and the ultimate homogeneity at the end of November.

TABLE V

Characteristics of the *Zostera noltii* vegetation under influence of grazing by birds in permanent plots (N = northern, E = eastern, S = southern and W = western plot). The number of shoots m^{-2} and the standing crop could only be determined for the ungrazed vegetation (i.e. on the first observation date), since grazing pressure was unequal between the above-ground and below-ground plant parts

Plot	Date	Cover (%)	Heterogeneity index	No. shoots m^{-2}	Standing crop (g dry wt.m^{-2})
N	30 September	46	30	45 800	2300
	3 November	26	45		
	27 November	2	0		
E	2 October	26	33	20 508	1032
	5 November	14	22		
	29 November	5	11		
S	8 October	22	34	15 200	766
	6 November	14	26		
	30 November	6	18		
W	9 October	32	31	23 200	1167
	7 November	15	19		
	30 November	4	5		

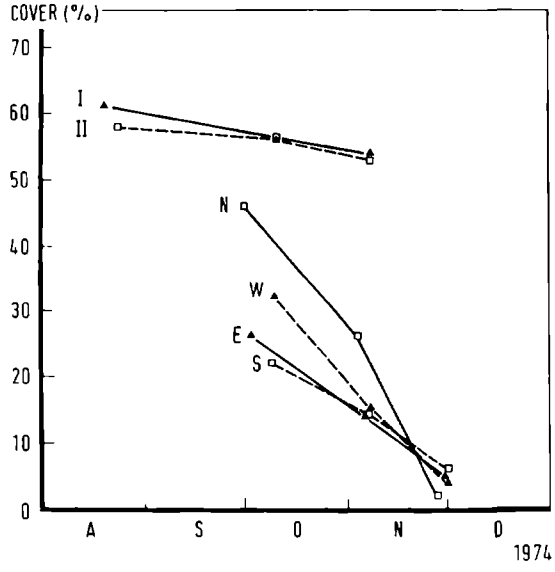

Fig. 5. The decrease in the percentage cover of *Zostera noltii* during the autumn of 1974 due to grazing by birds in the permanent plots (N, E, S, W), and in two enclosures (I and II).

creased. Continued grazing and erosion resulted in a homogeneous vegetation with a low percentage cover (see Table V and Figs. 4 and 5).

The changes of the seagrass vegetation described concern only the visible parts, i.e. the above-ground parts of the plants. Because of unequal grazing pressure between leaves and rhizomes, it is impossible to calculate the total standing crop at each mapping. Only for the first mapping could the total standing crop and the number of shoots m^{-2} of the vegetation be determined (see Table V).

The cover of the vegetation in the two enclosures during autumn is given in Fig. 5. The initial cover was relatively high and decreased only very slowly during the investigation period, whereas the heterogeneity index showed consistently low values, i.e. a homogeneous vegetation. The decreasing cover was a result of the natural process of dying-back of plants and breaking off of leaves by water currents. The average total biomass decreased from the end of August to the beginning of November in the enclosures I and II from 165 and 119 to 77 and 71 g dry wt. m^{-2}, respectively (i.e. 53% and 40% reduction).

DISCUSSION

Grazing pressure is primarily regulated by the food supply (Lack, 1954) and there is evidence that foraging birds will use their feeding grounds as optimal as possible in normal circumstances and in the absence of disturbance. Grazing pressure will also be influenced in a negative way by factors such as overshooting and disturbance which will reduce the population size of a species without decreasing the food supply. Disturbance can reduce grazing pressure, and Ranwell and Downing (1959) reported a decrease in cover of seagrass at Norfolk from October to April of only 70%, as a result of human disturbance.

The grazing pressure on the seagrass on the tidal flats near Terschelling seems to be optimal and natural. Comparison of our data with those of other seagrass beds is difficult, because the grazers and their distribution were the subject under investigation in most studies (Fog, 1967; Mörzer Bruyns and Timmerman, 1968; Maheo, 1976), or their supply of food (Butcher, 1941; Campbell, 1946; Mörzer Bruyns and Tanis, 1955; Olney, 1964; Wolff et al., 1976; Charman and Macey, 1978). However, Ranwell and Downing (1959), Burton (1961, 1962) and Wolff et al. (1967) showed a close correlation between the distribution of brent geese and the occurrence of their favourite food plants, *Zostera* spp., *Enteromorpha* spp. and *Ulva* spp. The effects of grazing on the seagrass itself have only recently been investigated (see for instance Charman, 1979). Only Nienhuis and van Ierland (1978), in a study of the consumption of eelgrass in Lake Grevelingen (SW. Netherlands), give any data. They demonstrated that 4% of the living *Zostera marina* production during summer was consumed by macroconsumers (0.92% by birds, the rest by *Idotea chelipes* Pallas). However, their investigation took place from 1 May to 31 August. Taking into account the fact that the wintering populations of herbivorous birds are many times larger than the summer ones, the amount of

eelgrass consumed on an annual basis could well be much higher. In addition, calculations and estimates on an annual basis are very difficult, because the eelgrass in Lake Grevelingen is of the annual form with almost no plants overwintering (Nienhuis and de Bree, 1977). Moreover, the grazing pressure in Lake Grevelingen from a bird point of view has to be of minimal value, because *Z. marina* grows there down to a depth of ca. 7 m, and is therefore inaccessible to the geese and swimming ducks.

Our investigation began with the arrival of the seagrass-consuming birds at Terschelling and continued until the cover of the seagrass had decreased to almost zero, i.e. until the above-ground parts of the plants had almost disappeared. It was calculated that the amount of *Zostera noltii* consumed during this period was approximately 50% of the total maximum standing stock. On the one hand the estimate can be considered somewhat low, because it was not possible to observe grazing during nightly low-water periods and on the other hand too high, because the grazing pressure on the above-ground parts was higher than on the below-ground parts (only the above-ground parts were involved in cover estimates). Therefore, the calculated amount of 50% seems a reasonable approximation. Since cover declined to almost zero, the remaining 50% of the maximum standing stock was consumed by invertebrates, broken off by wave action, died off naturally or overwintered as rhizomes until the following spring.

The influence of grazing by birds on the distribution and the morphological characteristics of the beds can be divided into short-term and long-term effects. Long-term influences concern the interactions between the population size of the birds and the spatial and temporal distribution of *Zostera*. For example the decline of *Zostera marina* in the 1930s, caused by the 'wasting disease' coincided with the decline of the brent goose (Mörzer Bruyns and Tanis, 1955; Ogilvie and Matthews, 1969; Charman, 1977). Trends in numbers of the geese since 1960 show a recovery of the world population in the 1970s (Maheo, 1976), despite an almost total disappearance of the *Z. marina* populations and a decline of *Z. noltii* in the Dutch Wadden Sea, as reported by Polderman and den Hartog (1975) and den Hartog and Polderman (1975). However, they believed pollution to be responsible for the decline. If there is a correlation between decreasing *Zostera* and increasing population size of the brent goose, then continued increase in the goose population will possibly result in an ultimate disappearance of all seagrass from the Dutch Wadden Sea, because the geese concentrate their feeding on *Zostera* and only after depletion of the stock do they graze other plants (Charman and Macey, 1978).

Short-term influences of grazing on the seagrasses concern the effects on vegetative and generative reproduction and on the process of growth and regeneration of the beds during and after grazing. The generative reproduction of *Z. noltii* is largely unaffected by grazing: seeds have already been produced before the majority of birds arrive at Terschelling. By grubbing and digging, the birds are likely to influence the seed dispersal in both a positive and negative way. Conversely, it could be argued that generative reproduction plays

little if any role in the maintenance of the beds and in the dispersal of the species, because seedlings are very rarely found inside the bed, as mentioned by den Hartog (1970).

It is apparent from the preceding discussion that only the consumption of rhizomes has a negative effect on the vegetative reproduction of *Z. noltii*. The grazing birds leave holes in the bed and after eroding and levelling by tide currents this results in a homogeneous vegetation pattern with in the midwinter period an ultimate cover of almost zero. In effect this means that the material accumulated between the plants during summer is washed away in the winter. The *Z. noltii* vegetation, therefore, plays little part (in the winter at least) in silt accumulation. The thinning out of the vegetation by birds leaves rhizome fragments, which overwinter. These remaining rhizomes develop in spring, with reduced intraspecific competition to form a new homogeneous mat of vegetation. It could be argued that, without grazing but with competition, self-shading and excessive silt accretion, the result after several years could be a raising of the bed above the high-water level, followed by a decline of the seagrass bed. In contrast, if the vegetation is grazed, sedimentation and erosion are on an annual basis in equilibrium and the seagrass beds survive.

ACKNOWLEDGEMENTS

We thank George Visser and his family for hospitality during our stay at the biological station "Schellingerland" at Terschelling and members of "Staatsbosbeheer" for their assistance with the building of the observation post. We are grateful to Ben Helming, Twan Thuyls, Erik van der Bilt, Arend van Dijk, Leo Zwarts, Meinte Engelmoer, Nelly van Brederode, Peter Esselink, Bert Brinkman, Joke Bloksma, Bruno Ens, Greetje Oostra and Kees Rappoldt, who assisted with counting birds on the island of Terschelling and on the tidal flats. We are also indebted to Dr. K. Charman, and to C. Swennen for critically reviewing the manuscript and to Mr. J.J.A. Slippens for the drawings. This study was financially supported by the "Beyerink-Popping" fund.

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ECOLOGICAL EFFECTS OF THE 'AMOCO CADIZ' OIL SPILL ON THE SEAGRASS ECOSYSTEM AT ROSCOFF, FRANCE

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ABSTRACT

The effects of the 'Amoco Cadiz' oil spill on the seagrass (Zostera marina) ecosystem at Roscoff, France, were studied during 13 months after the accident and compared to baseline data collected during a pre-spill period.

Detailed descriptions of population characteristics and productivity of the seagrass are presented in addition to data on species composition and abundance of the epiphytic algae. The impact of the oil on the seagrass was restricted to short-term, local effects evident by black leaves. The epiphytic algae appeared to be unaffected. A possible indirect effect of the oil on the general algal bloom a few months after the spill is discussed.

Qualitative and quantitative analysis of the macrofauna showed a selective influence on the different groups of animals. Some appeared unaffected, whereas others showed a decrease of both individuals and species.

Most species recovered rather quickly, attaining nearly their former levels by the beginning of 1979. Of the very diverse amphipod fauna, the filter feeders disappeared and were still absent on 1st May, 1979.

It is concluded that the seagrass ecosystem is a resistant unit, probably due to buffering effects of the plant community itself. The oil pollution caused only a short-term change in diversity without really affecting the stability of the ecosystem.

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INTRODUCTION

On 16th March 1978 the supertanker 'Amoco Cadiz' was wrecked on rocks near Portsall (Brittany), spilling about 220,000 tons of light Arabian and Iranian crude oil. As a result of the spreading oil, approximately 300 km of different types of shore were polluted to varying degrees.

Following the accident, numerous reports appeared covering a wide variety of biological, chemical, physical and geomorphological topics. Hess (1978), Conan et al. (1978) and Amoco Cadiz (1981) presented the most comprehensive summaries of impact and effects. Papers referring to the persistence of the oil in particular, include Hayes et al. (1979), D'Ozouville et al. (1979), Berné and D'Ozouville (1979), Law (1980), Berné et al. (1980), Gundlach et al. (1981) and Long et al. (1981). The clean-up operations were covered by Bellier and Massart (1979), Hann (1979), Bocard et al. (1979), Bellier (1979) and others.

It is possible to observe and/or map the physical or chemical features related to the oil spill almost directly, while analysis of the biological consequences appeared to be more diverse and complex, in other words time-consuming. Though the substratum and the physical coastal features largely determine the biological characteristics, the shoreline sensitivity to pollution is primarily related to these biological characteristics. Analysis of the ecological effects consisted of short-term studies to collect, identify and count the dead organisms, and long-term studies on the effects and the recovery of affected communities.

Direct toxicity was the easiest parameter to measure and several documents have been published with biological effects and numbers of dead organisms during the first weeks after the spill (e.g. Hope Jones et al., 1978; Swennen, 1978; Chassé and Morvan, 1978; Monnat, 1978; Chassé, 1979; Marchand et al., 1979; Laubier, 1980; Floc'h and Diouris, 1980). However, evaluation of the ecological impact on community or ecosystem level requires a more time-consuming assessment of fundamental and unifying concepts including structure, productivity, energy flow, stability, diversity, resistence and resilience. Several long-term, monitoring studies have been carried out at species or population level (e.g. Gooday, 1980; Koster and Van den Biggelaar, 1980; Noël, 1981) and at community or ecosystem level (e.g. Long and Vandermeulen, 1979; Dauvin, 1979, 1982; Gentil and Cabioch; 1979; Samain et al, 1979; Boucher, 1980; Cabioch, 1980; Cabioch et al., 1980; Vandermeulen et al., 1981; Raffin et al., 1981; Levasseur et al., 1981).

This paper deals with the effect on the eelgrass (Zostera marina L.) ecosystem at Roscoff. The oil slick reached Roscoff on 20th March and disturbed a research programme aimed at the study of structural and functional aspects of seagrass ecosystems. The project had commenced in 1976 and was continued into April 1979. The observations made before the spill provided reference data for the present study. The effects of the spill on the benthic fauna in the eelgrass meadow were summarized and presented in two preliminary reports (Jacobs, 1980; Den Hartog and Jacobs, 1980). The baseline data were published

by Jacobs (1979), Jacobs and Pierson (1979, 1981), Jacobs and Noten (1980) and Jacobs et al. (1983), and for detailed information about the study area, abiotic factors and methods applied, the reader is referred to these papers.

FLORA

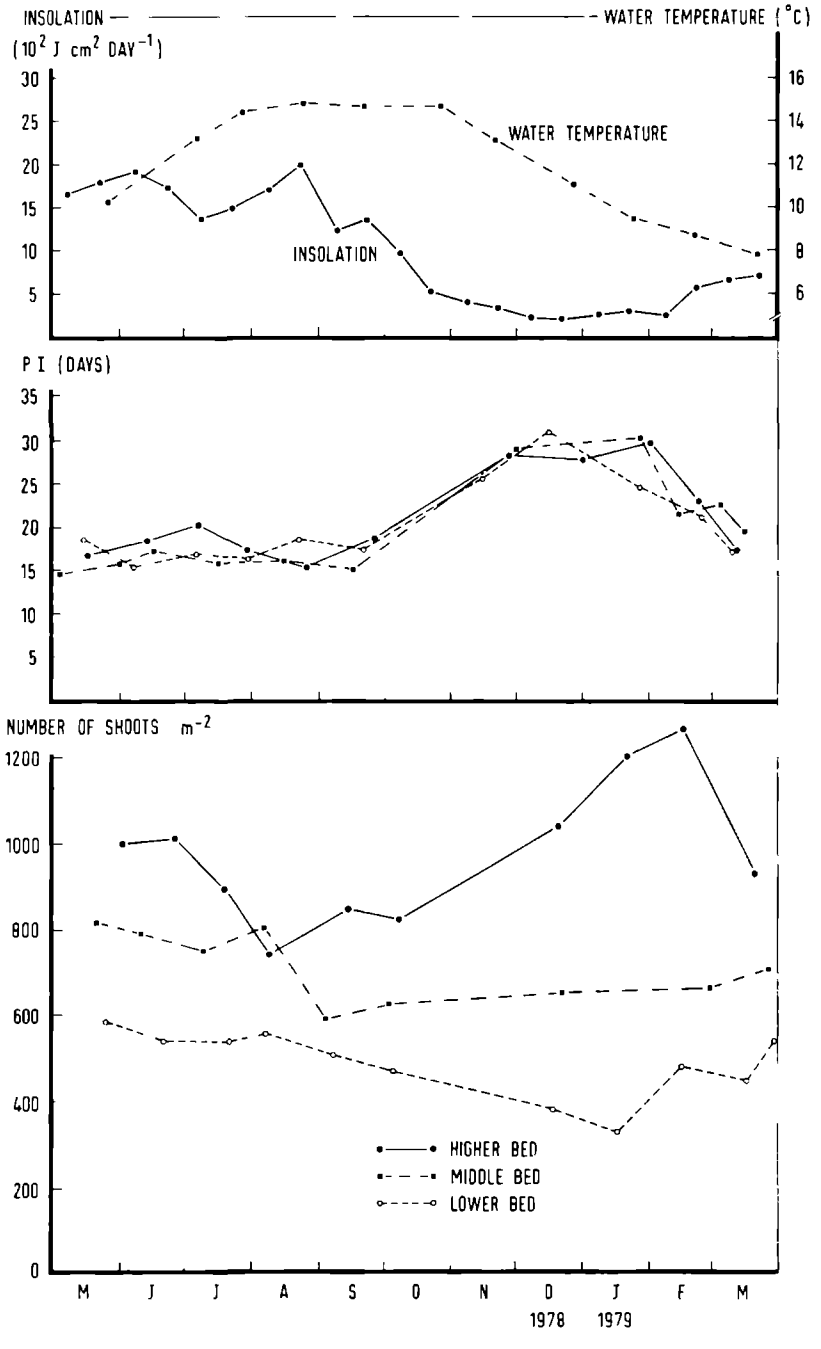
A seagrass ecosystem has to be regarded as a functional and structural unit, in which the seagrass population itself is the frame-element of the community structure. The most important additional structural elements are: (1) leaf-epiphytes and (2) rhizome-epiphytes on the seagrass plants, and (3) a mat of more or less loose-lying algae between the shoots. In Zostera beds no algae are found on the rhizomes, in contrast to, for example, in a Posidonia bed, where a luxurious vegetation of algae occurs on the vertically growing rhizomes (e.g. Boudouresque, 1974). The rather fluctuating species composition and abundance of the algae between the eelgrass shoots render this community element unsuitable for a study on the impact of oil on the system. Hence, a survey was made of only the seagrass and its epiphytes.

SEAGRASS

At Roscoff Zostera marina is distributed both in the littoral and sublittoral, from mean low water level at neap tide (MLWN) down to a depth of ± 4 m below mean low water level at spring tide (MLWS). On the 20th March 1978 the first oil reached Roscoff and remained visible during the week which followed. The thickness and extent of the oil slick varied from day to day, depending on currents and wind-direction. During low water periods other than during neap tide, oil covered the littoral eelgrass beds. However, during high water periods vertical transport processes always resulted in a loosening of the direct contact with the slick, the beds being situated below MLWN.

After a few days as the wind changed and came from a northern direction, the mass of oil visible on the water surface disappeared, though during low tide the littoral seagrass meadows were still covered with a thin, blue-tinted sheet of oil. In addition, a considerable amount of oil remained in the sediment, and came up to the water surface as one walked through the meadow. Stones and rocks at the high water level showed local, thick layers of brown or black oil residue.

During the months of April and May the impact on the seagrass was distinct: some leaves were black and looked 'burnt', whereas others were partly transparent. This phenomenon was especially apparent at the boundaries of the beds in the higher littoral, which were in direct contact with the slick for a maximum of 6 h a day. However, these leaves were shed according to the pattern normal for the species and the production of new leaves on these shoots continued in the characteristic manner (see Tomlinson, 1974; Sand-Jensen, 1975; Jacobs,


INSOLATION
WATER TEMPERATURE (°C)
(10² J cm² DAY⁻¹)
WATER TEMPERATURE
INSOLATION
P I (DAYS)
NUMBER OF SHOOTS m⁻²
HIGHER BED
MIDDLE BED
LOWER BED
M J J A S O N D J F M
1978 1979

1979). The general structure of the seagrass beds appeared to be unaffected. This supports the observations made by Calder et al. (1978), who measured considerable amounts of oil hydrocarbons in eelgrass at Portsall, though no damage was visible. In order to be able to establish possible influences of oil or oil compounds on the growth and production of eelgrass at Roscoff, several relevant features were investigated.

The fundamental parameter by which to describe the growth dynamics of Z. marina is the Plastochrone Interval (P.I.), i.e. the time interval between the initiation of two successive leaves on a shoot (Jacobs, 1979). The interval is independent of the standing crop and the number of shoots m^{-2} and may be considered a reflection of the actual condition of the plants in relation to their environment. As in 1976/1977 (see Jacobs, 1979, Fig. 8), the general trend of the P.I. appeared reversely correlated with the insolation pattern: the higher the quantum influx, the smaller the P.I. (see Fig. 1) and, consequently, the higher the production rate of leaves and rhizome segments. Apparently no direct correlation existed with the temperature (see Fig. 1). The P.I. values for 1976/1977 were determined in an eelgrass bed just to the south of Ile Verte (see Jacobs, 1979, Fig. 1). This meadow is indicated as the middle bed in the present study. The higher and lower bed were also situated in the same area, i.e. between Ile Verte and the shore. The height in the littoral of the three beds was measured as 1.9, 2.8 and 3.4 m above LLWS (low low water level at spring tide). These three levels were chosen because a possible impact would be expected to vary at different levels, depending on the period of direct contact between eelgrass and oil.

Comparing the P.I. curves for the three beds shown in Fig. 1, the line for the higher bed most closely correlates with the insolation pattern. The others show a more gradual course at intermediate levels, probably due to diminished effects of insolation fluctuations as a consequence of the water layer above the vegetation. The P.I. values, averaged for the three beds for the period May to October, ranged from 14.7 to 20.3 days, and for the second half of the investigation period from 17.1 to 31.0 days. These values appear to be comparable with the data collected in 1976/1977, when an average P.I. of 19.3 days was measured, with a minimum of 13 days in May and a maximum of approximately 28 days in December.

In addition to variations in production rate of rhizome segments,

Fig. 1. Seasonal variation of the Plastochrone Interval (P.I.) and the shoot density of Zostera marina at Roscoff after the oil spill, estimated in the higher, middle and lower bed, situated at about 3.4, 2.8 and 1.9 m above LLWS level, respectively (all figures represent average values of four determinations). The insolation pattern (average over 15 day periods) and water temperature are shown in the upper figure.

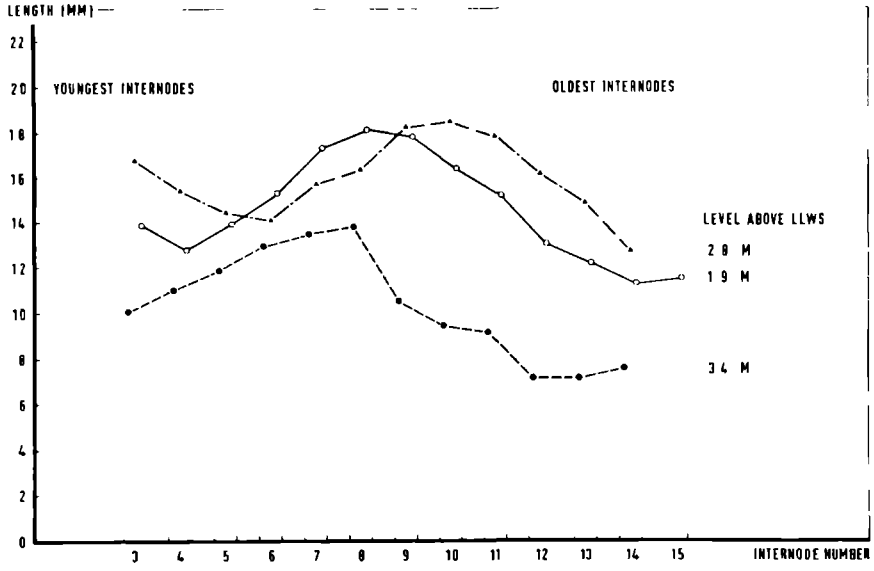


Fig. 2. Variation in the average length of the internodes of Zostera marina rhizomes in the three distinguished littoral beds, dug out in the first half of September 1978. For explanation see text.

the length of the segments fluctuated in 1976/1977 (see Jacobs, 1979, Fig. 7). The characteristics of the eelgrass rhizomes in the three beds were investigated on plants dug out in September 1978; each rhizome segment was measured. The maximum numbers of living segments per plant appeared to be 15. The curves resulting from the temporal variations in length are presented in Fig. 2. The values for the higher bed appeared considerably lower than those for the other beds which were not significantly different. By examining these curves in relation to the length of the Plastochrone Interval (Fig. 1), the time of initiation of each particular segment can be calculated. The oldest, shortest internodes were produced in the 1977/1978 winter. The lengths subsequently reached a maximum in May and June, and decreased in July. The last produced segments showed an increasing length. This temporal pattern closely agreed with the curves for the insolation and the P.I. (compare with Fig. 1).

A directly perceptible character of the eelgrass population was the shoot density (see Fig. 1). During summer 1978 an overall decreasing number of shoots was observed, especially in the higher bed. As this bed was situated at the higher limit of occurrence in the littoral, it was permanently exposed to physical influences determining the upper limit, resulting in a dynamic equilibrium of colonization of bare substrates and destruction by currents. During the summer of 1978 the last phenomenon was intensified because the leaves were heavily overgrown by epiphytic algae, making the shoots particularly vulnerable.

TABLE 1

Comparison of temporal changes in shoot density of Zostera marina at three tidal levels (3.4, 2.8 and 1.9 m above LLWS level).

Zostera bed	Period	Number of shoots m^{-2} av.	min.	max.
higher (+3.4 m)	Nov. 1977 - April 1978	775	450	1000
	May 1978 - Oct. 1978	862	750	1000
	Nov. 1978 - April 1979	1091	925	1256
middle (+2.8 m)	April 1976 - Aug. 1976	688	550	733
	Nov. 1977 - April 1978	650	600	725
	May 1978 - Oct. 1978	724	550	800
	Nov. 1978 - April 1979	654	550	710
lower (+1.9 m)	Nov. 1977 - April 1978	625	475	900
	May 1978 - Oct. 1978	523	475	571
	Nov. 1978 - April 1979	429	325	531

TABLE 2

Production of Zostera marina at Roscoff in the three distinguished littoral beds (3.4, 2.8 and 1.9 m above LLWS level).

Zostera bed	Period	Production (g dry wt m^{-2} day^{-1})	Above-ground production
higher	May 1978 - Oct. 1978	4.2	71%
	Nov. 1978 - April 1979	2.1	83%
middle	May 1978 - Oct. 1978	5.4	66%
	Nov. 1978 - April 1979	1.9	81%
lower	May 1978 - Oct. 1978	5.0	68%
	Nov. 1978 - April 1979	0.9	77%

As in 1976/1977 (see Jacobs, 1979, Fig. 7), new shoots were produced in spring and after a sharp decrease in July 1978, a second production period was observed in September, with the highest numbers of new shoots in the middle bed. The increases in shoot density both concurred with increases in insolation (see Fig. 1), suggesting a direct correlation.

In Table 1 the population dynamics since 1976 are presented in terms of numbers of shoots per m^2. The density in the middle bed appeared constant throughout the years, ranging from 550 to 800. The situation in the higher and lower beds was different. In the higher bed the shoot density increased from 1977 onwards. As shoot density decreased with increasing tidal depth (see Fig. 1), it may be concluded that the level of the higher bed gradually raised during the years. This assumption was confirmed by field observations. During the whole year, particularly autumn, sand settled on the bottom as the currents in which it was carried were obstructed by the seagrass shoots. The more or less horizontally growing rhizomes colonized this newly deposited substrate. Raising of the beds resulted in an increased exposure of the boundaries to currents, which undermined the rhizome mat so that parts of the bed were subsequently torn apart. The decrease in the number of shoots in the lower bed from 1977 (see Table 1) might be caused by a lowering of that meadow.

Examination of the total eelgrass production in 1978/1979 (Table 2), shows values comparable to those for 1976/1977 (see Jacobs, 1979, Fig. 9). The annual production was highest in the middle bed. The autumn and winter production seemed to be correlated with the height in the littoral and decreased with increasing depth. During that part of the year the above-ground production amounted to approximately 80% of the total production, while in spring and summer it was ± 70% (Table 2).

ALGAE

The study on the epiphytic algae of Zostera marina was carried out from May to October 1978, and the methods were identical to those applied in 1976/1977 (see Jacobs et al., 1983). Only the results concerning the situation in the middle bed are presented in Table 3. Examining these results two characteristics can be noted:

- The species richness in the higher bed was smaller than in the other beds at each sampling date.
- The frequency of occurrence of the Rhodophyceae increased with tidal depth. Taking into account the relation between the spectral composition of light depending on the water depth and the composition of photosynthetic pigments of the algae, this general trend could be expected.

Comparison of the results of the two periods brings to light:

- The occurrence and abundance of the pioneer taxa in the epiphytic association, i.e. Audouinella virgatula, Fosliella lejolisii, Myrionema magnusii and the diatoms, and their colonization patterns were comparable for both periods.

- In addition to the pioneer taxa, Rhodophysema georgii and Ectocarpus spp. appeared to form a characteristic element of the epiphytic vegetation during the period of investigation, the first mainly occurring on the edges of older leaves.
- In general the species composition was identical. However, Rhodophysema georgii was not found in 1976/1977 and seems to be restricted to particular years. Den Hartog (1976) mentioned the species as a characteristic epiphyte of eelgrass at Roscoff. Other species not found in 1976/1977 were the brown algae Scytosiphon lomentaria and Giffordia mitchelliae (Harv.) Hamel. The last species was found on shoots collected from sublittoral stands during an investigation into the spatial distribution of the epiphytes.
- During June and July an exceptional growth of Ectocarpus spp. was observed, reaching cover values of more than 100% on the eelgrass leaves.

TABLE 3

'Presence table' of the epiphytic algae on Zostera marina in the midlittoral bed (1 = presence in 1-20% of the relevés; 2 = 21-40%; 3 = 41-60%; 4 = 61-80%; 5 = 81-100%).

Month (1978)	May	June	July	Aug.	Sep.	Oct.
Species						
Audouinella virgatula (Harv.) Dixon (R)*	5	5	4	5	5	5
Bacillariophyceae	5	4	4	4	3	1
Fosliella lejolisii (Rosan.) Howe (R)	1	1	1	3	5	5
Myrionema magnusii (Sauv.) Lois. (P)	2	4	3	4	2	3
Ectocarpus spp. (P)	4	4	2	2	2	1
Rhodophysema georgii Batt. (R)	3	2	2	4	4	3
Ceramium rubrum (Huds.) C. Ag. (R)	2	2	1	1		1
Erythrotrichia boryana (Mont.) Berth. (R)	2	2	1	1	2	
Erythrotrichia carnea (Dillw.) J. Ag. (R)	2	1		4	4	2
Ulothrix spp. (C)	3	1				
Chlorophyceae spp. (young)		1	1			
Asperococcus c.f. turneri (Sm.) Hook. (P)		1	1	1		
Punctaria tenuissima (C. Ag.) Grev. (P)		1				
Scytosiphon lomentaria (Lyngb.) Link (P)	1					
Myriotrichia clavaeformis Harv. (P)				4		
Cyanophyceae		3				

*C = Chlorophyceae; P = Phaeophyceae; R = Rhodophyceae

Ectocarpus spp., Enteromorpha spp., Ulva spp. and Ceramium rubrum quickly colonized many substrates in June and July.

TABLE 4

Biomass (g ash-free dry wt m^{-2}) of herbivorous gastropods in the middle Zostera marina bed. The total numbers of individuals m^{-2} of the dominant Gibbula species are given in the lower part. All figures represent average values of 3 samples (1 m^2); p = species present, biomass too low for determination.

Month (1978)	May	June	July	Aug.	Sep.
Species					
Barleeia unifasciata (Montagu)		p	p	p	p
Calliostoma zizyphinum (L.)	100	229			48
Catharidus striatus (L.)		4.3	6.5	1.8	
Cingulopsis fulgida (Adams)					p
Gibbula cineraria (L.)	354	1127	362	1022	659
Gibbula pennanti (Philippi)	4148	7619	4224	5378	7581
Gibbula umbilicalis (Da Costa)	30	28			
Hydrobia ulvae (Pennant)	p				
Lacuna vincta (Montagu)			2	2	9
Littorina obtusata (L.)		11	22	50	35
Onoba semicostata (Montagu)	p				
Patella vulgata L.			p		
Patina pellucida (L.)		p		p	p
Rissoa guerini Récluz	0.7	p		p	p
Rissoa membranacea (Adams)	0.6	p	0.9	p	9.5
Rissoa parva (Da Costa)	0.9	p	p	p	p
Tricolia pullus (L.)					6.5
No. ind. m^{-2}					
Gibbula cineraria	11	22	10	20	20
Gibbula pennanti	33	74	50	48	85
Total	49	120	100	105	144

The exceptional growth of these algae was a local phenomenon (Marchand et al., 1979), different from the 'greening' after the 'Torrey Canyon' spill (Southward and Southward, 1978). An algal bloom is a normal annual phenomenon at Roscoff, occurring with an increase in available nutrients after winter and an increase in temperature and irradiation in spring. However, the extent of the bloom was greater than in preceding years. Various factors or a combination thereof may be responsible: (1) stimulating effects of oil components in low concentrations (GESAMP, 1977), (2) increase in nutrients originating from oil-killed organisms, and (3) a reduced population size of herbivorous animals. In an attempt to discern the effects of the different factors mentioned, a major group of herbivores, the gastropods, was investigated in detail. Before the oil spill the

numerically dominant gastropod in the middle eelgrass bed was the very small snail Onoba semicostata, whereas the widely occurring species of the genus Gibbula were most important from a functional point of view, as was the less numerous Calliostoma zizyphinum. After the spill the Gibbula species comprised an average of 73% of the total number of gastropod species and 98% of the total biomass (see Table 4). Although the results in Table 4 represent average values calculated from 3 square metres, the data somewhat fluctuated with time. Nevertheless, the overall picture does not really deviate from the situation over the same period in 1977 (see p. 194). It would thus seem justified to conclude that the factors determining the algal bloom, were directly related with nutrient enrichment or stimulation by low concentrations of oil.

FAUNA

From October 1977 to April 1979 a bottom sample of 20 x 20 cm was taken monthly in the higher and middle Zostera bed in order to study the fauna. For a detailed description of the method applied see p. 99. In the laboratory these samples were sieved through 1 mm mesh and all organisms were collected and preserved. Special attention was paid to tufts of algae and tunicate colonies in the samples. These were thoroughly sifted in water, sometimes with addition of a little

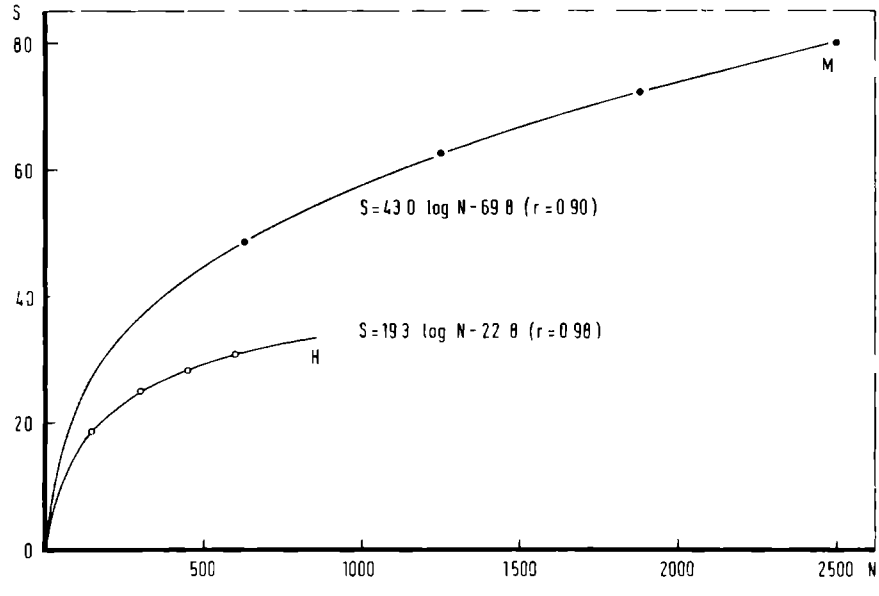


Fig. 3. Calculated relationships between the number of species (S) and individuals (N) for the fauna in the higher (H) and middle (M) Zostera marina bed. Samples were taken simultaneously in January and February 1979 in the higher and middle bed, respectively.

TABLE 5

Numbers per 400 cm^2 of individuals and of species (in parentheses) of the dominant fauna groups in the higher (upper table) and middle (lower table) Zostera marina bed at Roscoff, before and after the oil spill of the 'Amoco Cadiz'.

	1977			1978											1979			
Group	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
Polychaeta Errantia	18(5)	38(5)	25(6)	13(7)	19(6)	21(7)	14(6)	23(4)	16(5)	18(5)	30(6)	15)	24(3)	22(3)	11(5)	15(5)	16(4)	14(4)	12(3)
Polychaeta Sedentaria	85(10)	113(9)	219(8)	101(9)	114(8)	152(9)	41(4)	66(7)	51(5)	75(7)	9(8)	68(11)	36(6)	72(10)	111(12)	95(11)	61(10)	79(9)	109(9)
Decapoda Reptantia	6(2)	5(2)	1(1)	1(1)	3(1)	4(1)	1(1)		3(1)	10(1)	9(2)	3(2)	1(1)	5(1)	6(2)	1(1)			1(1)
Amphipoda	6(3)			1(1)	1(1)						15(2)				1(1)		1(1)	5(2)	
Tanaidacea	218(1)	113(2)	22(1)	69(1)	52(1)	62(1)	7(1)	1(1)	2(1)	2(1)	8(1)	30(1)	5(1)	11(1)	9(1)	19(1)	2(1)	4(1)	20(1)
Gastropoda	3(2)	5(4)	2(2)	3(1)	1(1)	3(2)	2(2)		1(1)	4(3)	1(1)	3(2)	3(2)	6(2)		2(1)			
Bivalvia	49(2)	56(3)	26(4)	12(2)	36(3)	24(3)	44(2)	66(2)	41(2)	37(3)	56(3)	39(1)	14(2)	32(2)	41(2)	42(1)	47(3)	74(3)	72(2)
Echinodermata	12(1)	17(1)	13(1)	1(1)															

	1977			1978											1979			
Group	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
Polychaeta Errantia	22(5)	58(8)	22(4)	34(7)	19(4)	31(7)	20(4)	16(5)	96(7)	34(3)	29(5)	43(6)	42(3)	50(4)	22(3)	16(5)	37(7)	46(8)	18(7)
Polychaeta Sedentaria	109(6)	206(10)	113(8)	105(10)	147(9)	90(10)	55(6)	31(8)	25(5)	35(6)	30(6)	47(6)	43(6)	104(7)	67(8)	30(9)	63(10)	54(9)	75(8)
Decapoda Reptantia	20(6)	2(2)	9(3)	1(1)	6(3)	4(2)	1(1)		21(4)	7(2)	12(1)	9(3)	6(3)	4(2)	11(3)		3(2)	6(4)	1(1)
Amphipoda	25(10)	28(8)	16(9)	16(11)	160(21)	120(20)	5(2)		3(3)			8(1)	5(1)	2(1)	10(2)	19(3)	31(6)	37(5)	12(2)
Tanaidacea	231(2)	259(2)	121(3)	80(3)	416(3)	282(3)	62(3)	6(1)	12(2)	6(1)	5(1)	42(1)	68(1)	238(1)	214(1)	92(2)	122(2)	177(1)	337(1)
Gastropoda	20(8)	53(5)	15(6)	156(5)	141(15)	69(7)	49(9)	17(4)	44(8)	21(6)	16(10)	13(7)	17(7)	7(3)	7(4)	12(2)	196(9)	79(13)	125(10)
Bivalvia	24(3)	56(5)	12(5)	32(4)	26(5)	6(5)	13(4)	9(5)	6(4)	2(1)	10(3)	4(4)	3(3)	16(4)	8(4)	3(2)	10(5)	18(4)	18(6)
Echinodermata	72(1)	210(1)	190(1)	120(1)	179(2)	134(1)	164(2)	20(1)	12(1)	7(1)	19(1)	37(1)	27(1)	20(1)	43(1)	41(1)	47(1)	82(1)	85(1)

formalin to expel the amphipods. After identification to species level, each sample was characterized by four parameters: number of species (S), number of individuals (N), calculated species diversity (H) and evenness (J) (Pielou, 1969). Though all Porifera and Tunicata were identified, quantification of the specimens was not possible.

Since most diversity measurements are affected by sample size, the latter was kept constant in order to be able to compare samples taken in different seasons. Comparison of four samples of 20 x 20 cm, taken simultaneously in January 1979 in the higher and in February in the middle bed, showed a random or aggregated distribution of the individuals for 99% of all species. Using these samples the arithmetic means for both N and S of all combinations of samples were calculated for increased sample size. Subsequently, the specific relationships between numbers of species and numbers of individuals were determined (see Fig. 3). From the extracted r-values (i.e. 0.90 and 0.98 for the middle and higher bed, respectively) it can be concluded that the parameters were closely correlated to one another. From the shape of the species accumulation curves (Fig. 3) it can be derived that the saturation levels were not even attained with a sample size of 1600 cm^2. This may be attributed to the occurrence of many species with a low population density. This was especially apparent in the faunal assemblage in the middle bed, expressed by a curve with a slope of 43.0, this being only 19.3 for the higher bed (see Fig. 3). The number of species per sample was calculated to be approximately 65% of the total number of species actually present in the beds. These results showed that samples from the same bed in two succeeding months should be considered as one sample, in order to exclude fluctuations caused by incidentally recorded species. This approach was chosen particularly for data dealing with numerically important species or taxonomically related groups. At first a general picture of the results is presented and subsequently more detailed data of particular groups are reported and discussed in taxonomical order. All species found in the samples during the entire investigation period are presented in Table 6, in addition to their frequency of occurrence (in numbers of months).

The fauna in the higher eelgrass bed showed a decrease in both total numbers of individuals and of species at the end of 1977 (Fig. 4). This would appear to result from the increased sedimentation and a raising of the bed (see p. 180). This phenomenon might contribute to the lower values for S and N. The first samples after the 'Amoco Cadiz' oil spill showed a numerical decrease in species. Further, only half of the numbers of individuals present before the spill were found. This resulted in a decrease of the diversity index from 2.3 in March to 1.7 in May 1978 (Fig. 4a). After May the diversity recovered within three months. During the investigation period the S and N values never reached the values recorded before the spill.

Having first sharply decreased, the S and N values in the middle bed recovered gradually and continued to fluctuate slightly during further observation in 1978 and 1979, just as the diversity indices (Fig. 4b). This indicates that the community, disturbed just after the spill, regained a certain degree of stability in the beginning of 1979.

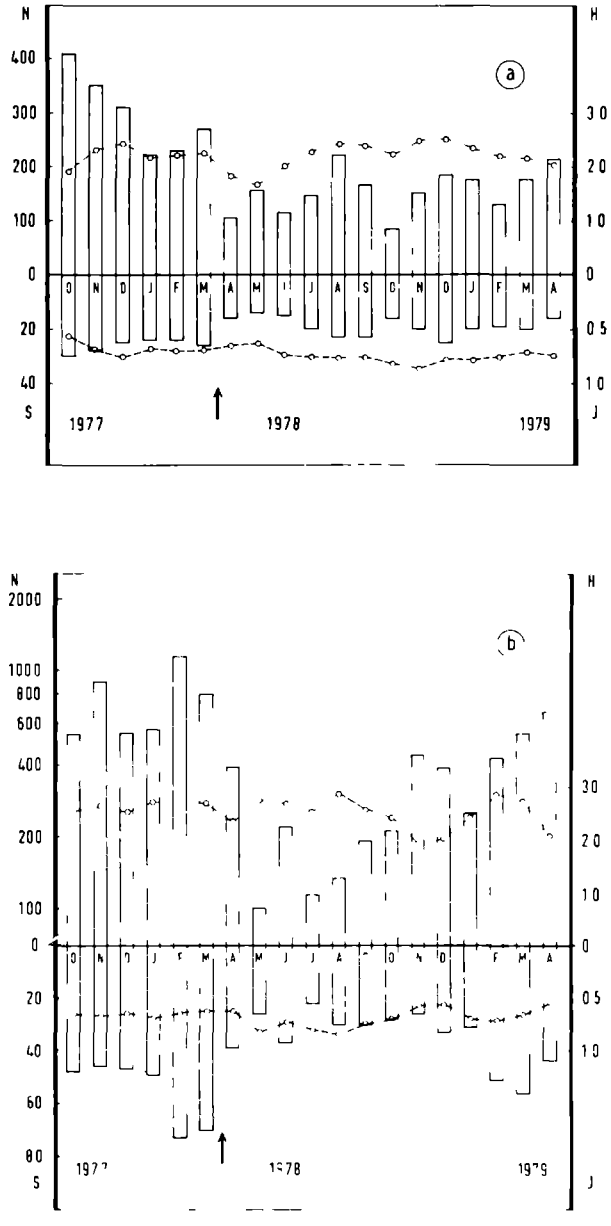


Fig. 4. Characteristics of the fauna of the higher (a) and middle (b) Zostera marina bed before and after the oil spill of the 'Amoco Cadiz'. Total numbers per 400 cm^2 of individuals (N) and of species (S), calculated diversity index (H) and evenness (J) given as broken lines. Arrow: moment of oil arrival at Roscoff.

The prominent decrease of the numbers of individuals and of species was mainly caused by the virtual disappearance of Amphipoda, Tanaidacea and Echinodermata. The numbers of Gastropoda, Polychaeta Sedentaria and Bivalvia also decreased (Table 5). Although recovery of the last mentioned groups in the middle bed proceeded from late summer onwards, the high spring maximum of 1978 was not reached in 1979. Though the Tanaidacea and Echinodermata recovered slower, the only exception in the described process was formed by the filter feeding Amphipoda, which had not returned in April 1979 (Table 5).

Porifera

The group of sponges was represented by 6 species (Table 6), of which Halichondria spp. and Hymeniacidon perlevis were characteristic inhabitants of the middle bed in particular. Both before and after the spill the sponges were found rarely and in fluctuating quantities.

Anthozoa

The sea-anemones seemed to be unaffected. Of all the species (Table 6), Halcampa chrysanthellum was found most regularly, though in small quantities.

Hydrozoa

The hydroid Haliclystus auricula (Rathke), an epizoan on Zostera, was occasionally found during the investigation period.

Polychaeta Errantia

During the study 24 species were recorded (Table 6). Common inhabitants of the seagrass beds were Phyllodoce mucosa, Platynereis dumerilii, Sthenelais boa and Lumbrineris latreilli. Only the first two species were also abundant in bare substrates outside the beds. The species Nephtys cirrosa Ehlers, Marphysa fallax Marion & Bobretzky and Protodorvillea kefersteini (McIntosh) were found exclusively outside the beds.

Effects of the spill on species richness and abundance could not be detected. With respect to the dominant representatives of the Nereidae this is not surprising, as these species are reported to be highly resistant to oil pollution (Kasymov and Alieu, 1973; Leppakoski and Lindstrom, 1978). In fact, the higher numbers of individuals in June (see Table 5) were a result of the settling of juveniles of the nereid species Platynereis dumerilii (compare with Fig. 5). This herbivorous polychaete is a typically epifaunal species, especially associated with eelgrass (Day, 1973; Rasmussen, 1973; Jacobs and Pierson, 1979) and algal communities. The increase in abundance concurred with the earlier described algal bloom. The species may well have attributed to a control of the bloom. Toward the end of 1978 the population size had returned to the level found before the spill (Fig. 5).

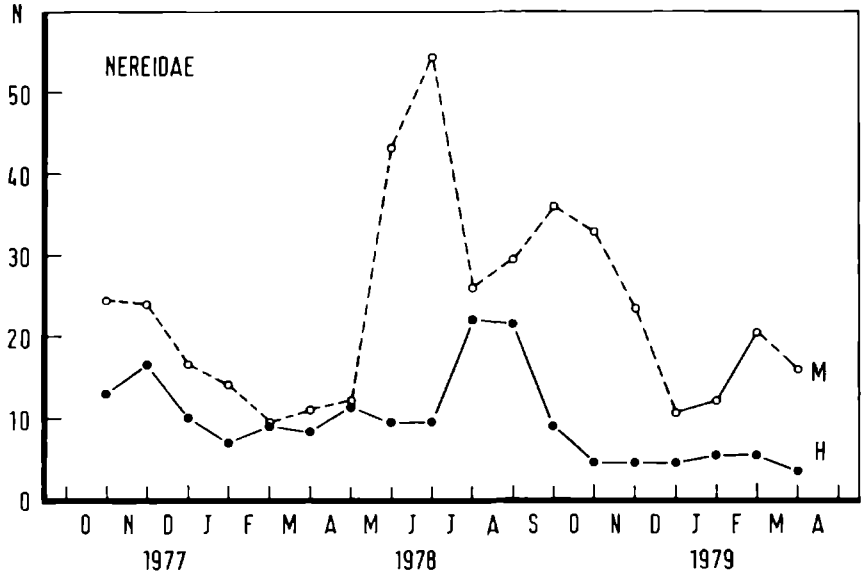


Fig. 5. Total number of individuals per 400 cm^2 (as an average of 2 successive months) of particular groups of animals in the higher (H) and middle (M) Zostera marina bed, before and after the oil spill of the 'Amoco Cadiz'.

Polychaeta Sedentaria

As shown in Table 5, the abundance of the Polychaeta Sedentaria decreased significantly after the oil spill. Recovery continued to the end of 1978, when the numbers in the higher bed were at a level comparable to the situation before the spill. However, the numbers in the middle bed remained consistently lower.

Of the 28 species found in the eelgrass beds (Table 6) the most dominant were the capitellids Notomastus latericeus and Heteromastus filiformis, the spionids Aonides oxycephala, Spio filicornis and Polydora flava, and the maldanid Euclymene sp., of which the majority belonged to Euclymene oerstedi and a few specimens to E. c.f. affinis.

Representatives of the spionids (Fig. 6) were highly affected during the first weeks after the spill. During the following months the numbers of all species increased. The higher abundance in summer and autumn was related with the establishment of Spio filicornis and Malococeros fuliginosus, of which the latter were previously rarely found. As M. fuliginosus, which originates from planktonic larvae, may settle very abruptly and in large quantities (Jacobs and Dubbers, 1980), it seems incorrect to regard it as an invading, opportunistic species.

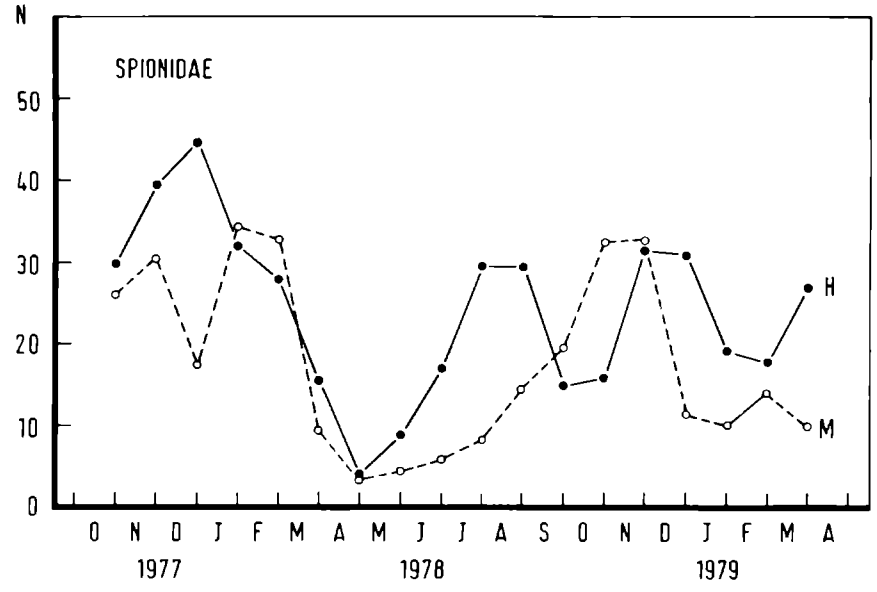


Fig. 6. See legend Figure 5.

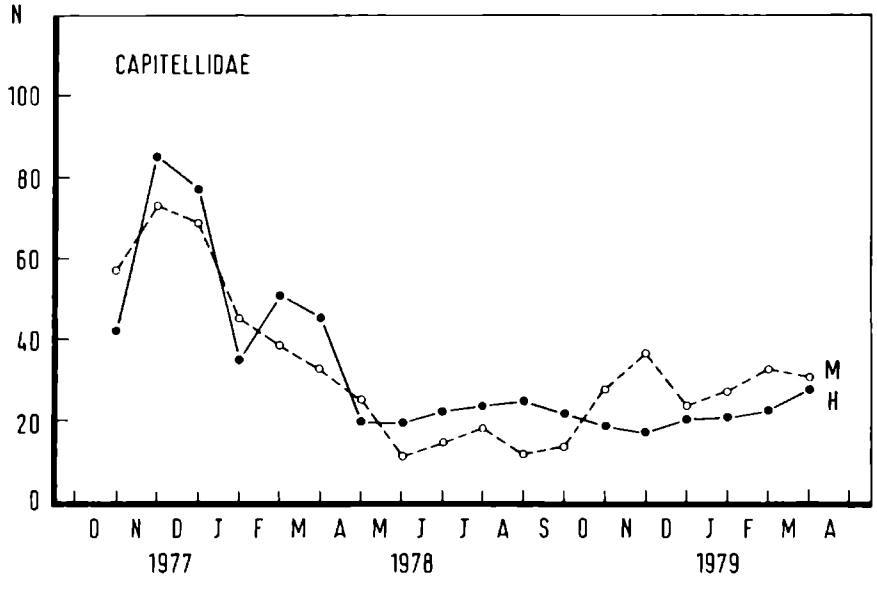


Fig. 7. See legend Figure 5.

Representatives of the Cirratulidae, particularly Cirriformia tentaculata, were found to be the first colonizers in heavily polluted areas (pers. obs., June 1978, Portsall). They apparently tolerate high concentrations of petroleum hydrocarbons without any effect on the spawning, growth and mortality (George, 1970, 1971). Their low numbers in the seagrass beds at Roscoff, even after March 1978, suggest a low level of pollution in the ecosystem.

The Capitellidae comprised the majority of the sedentary worms, only represented by three species, of which Notomastus latericeus dominated. Quantitative changes in the numbers after the pollution were immediately distinct (see Fig. 7). Recovery to values recorded before the spill was observed during the investigation period. Although Reish (1965, 1971) mentioned Capitella capitata as a very resistant, opportunistic species, consistently low numbers were found. However, the population density seems to be determined mainly by the nutritional value of available detritus. Tenore (1975, 1977a, b) stressed the role of C. capitata in detritus-based food chains, especially with respect to detritus derived from eelgrass.

The population of the maldanid Euclymene decreased evidently after the spill (Fig. 8) and continued to fluctuate at a lower density. The population in the middle bed was affected the most.

The families of the terebellids and sabellids were represented by 10 species, of which only Megalomma linaresi and Aphitritides gracilis occurred regularly. All species were again found after the spill, though in somewhat reduced numbers.

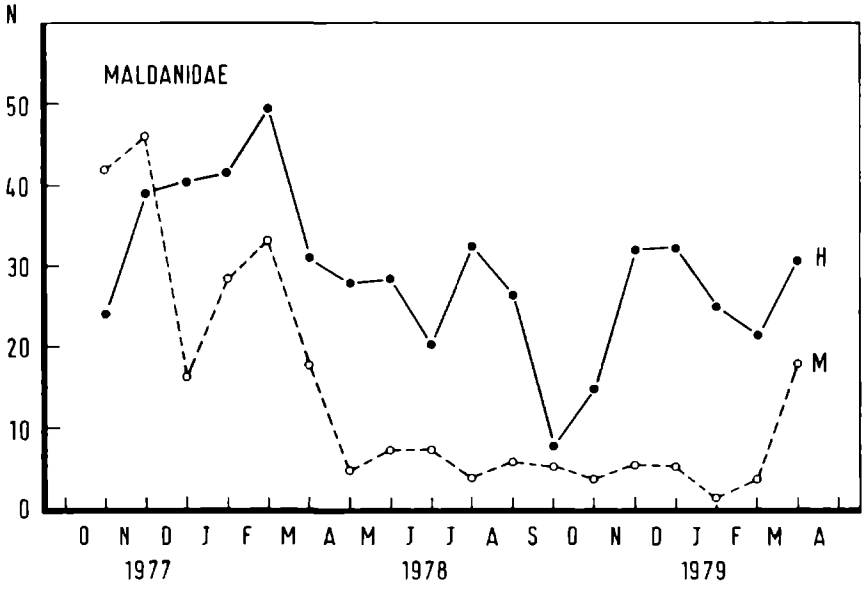


Fig. 8. See legend Figure 5.

The common members of this polychaete group are non-selective deposit feeders or burrowers (Capitellidae, Maldanidae) and selective deposit feeders (Spionidae, Terebellidae). It appears difficult to relate the reduction in population size of particular species to their feeding type. Burrowers may be hindered by oil pollution, at the same time resuspending oil incorporated into the sediments by their activities (Rhoads and Young, 1971). On the contrary, penetration of oil in the sediment of the seagrass bed is reduced by the thick rhizome mat. Filter feeders (Sabellidae) and selective deposit feeders are in direct contact with high-toxic, dissolved oil compounds and would be expected to be more susceptible. However, this is not confirmed by the results of this study, but may be explained by the relatively short exposure time and/or the sheltered habitat created by the seagrass.

Sipunculida

Both species (Table 6) were irregularly detected in very low numbers during the study.

Pycnogonida

The sea-spiders, generally sublittoral ectoparasites penetrating into the tidal area, were found exclusively in the middle bed. Only a few representatives were found of the five species (see Table 6), Nymphon gracile being the most widely distributed.

Decapoda

During the investigation period 14 species were recorded, Carcinus maenas being the most common. As the sampling method did not adequately register these mobile species, no quantitative evaluation of the results is possible. All species recorded before the spill were also found after March 1978. However, the low numbers do not justify any conclusions about possible effects of the spill.

In addition to the normal sampling programme several samples were taken with a dipping net. This resulted in the addition of the following species Hippolyte prideauxiana Leach, Palaemon serratus (Pennant), Anapagurus hyndmanni (Bell), Galathea squamifera Leach, Philocheras fasciatus (Risso) Eurynome spinosa Hailstone and Macropodia egyptia (Milne-Edwards). However, again the resulting species abundance appeared too low to allow analysis with respect to possible impact.

A detailed analysis of the population of Processa edulis in the eelgrass beds was given by Noël (1981), who found an important diminution as a result of the oil spill.

Amphipoda

Besides a few specimens in the higher bed, a diverse group of the amphipods was found in the middle bed, particularly during winter (Table 5 and 6). After the oil spill nearly all species

disappeared and only a few returned in the autumn of 1978, with Pherusa fucicola in rather high numbers (compare with Fig. 9). A species not observed before the spill was the ubiquitous

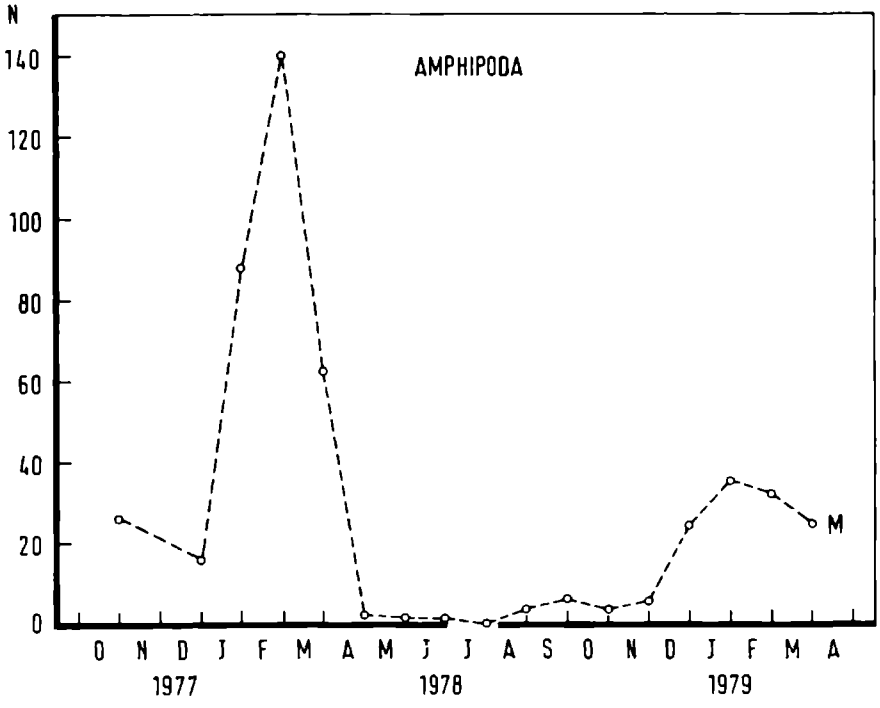


Fig. 9. See legend Figure 5.

Gammarus locusta. Most of the species adversely affected by the oil were filter feeders. After the Amoco Cadiz oil spill Dauvin (1979) reported a nearly complete disappearance of the amphipods in the Bay of Morlaix. The sensitivity of the amphipods varies with the species examined, but is greater than that of polychaetes or decapods (Lee et al., 1977).

Cumacea

The only species frequently recorded, particularly in the middle bed, was Iphinoe tenella. After March 1978 it disappeared and was not found until the winter of 1978/1979, when it showed a comparable species density.

Tanaidacea

Apseudes latreillei was distributed throughout the beds. After the oil spill the numbers showed a sharp decrease (Table 5, Fig. 10), followed by a complete recovery in the middle bed before the end of 1978. In the higher bed the population remained at a low abundance level. This may have been caused by the continuous sanding-up of the bottom, because the animals generally occur in the upper few centimetres. The two other species (see Table 6) were also affected by the oil, and only Aspeudes talpa returned in low numbers at the end of

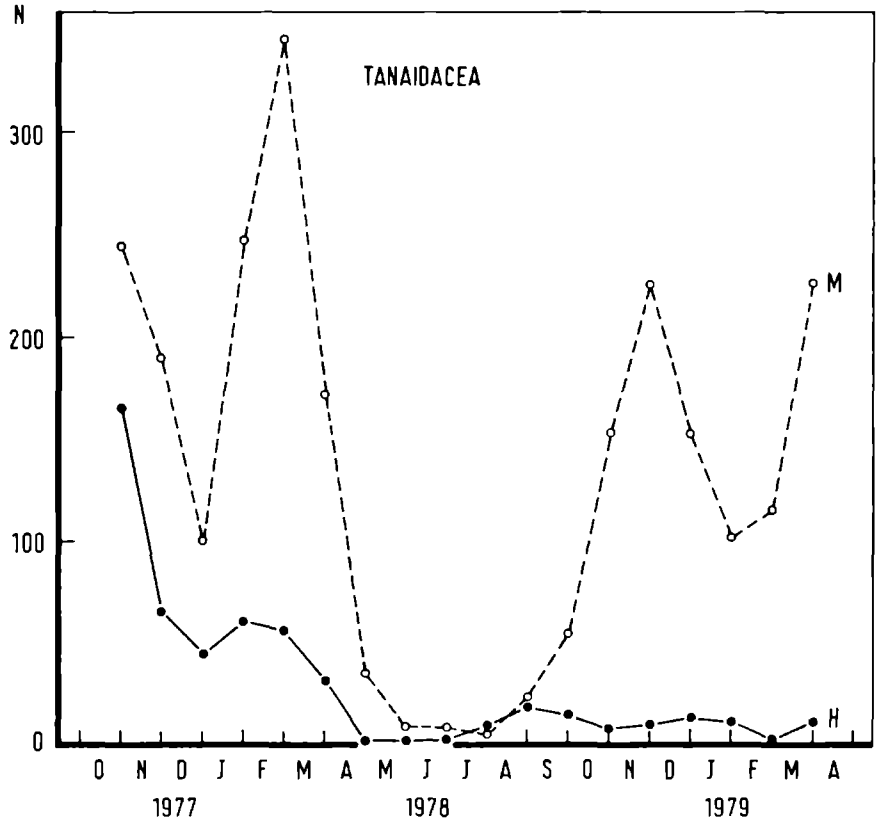


Fig. 10. See legend Figure 5.

1978. In November and December 1977 numerous juveniles of the Tanaidacea were found. These animals and the offspring of the first generation of 1978 were apparently highly affected by the oil. There may be three generations a year, as reported by Salvat (1967), a winter, spring and summer generation. From the results presented in Fig. 10 it can be concluded that the summer generation of 1978 was extremely small, due to the oil pollution.

Isopoda

Six species were found in very low numbers during the initial study (Table 6). During the 6 months after the spill not a single isopod was observed, and in the winter of 1978/1979 only 4 specimens, representing 4 species, were found. In fact the low numbers do not allow any conclusion about the influences of the spill. Recolonization may take a long time due to the poor mobility of the animals (see also Notini, 1980).

Gastropoda

The gastropods formed a most diverse group (Table 6), with the highest numbers of individuals and of species in the middle bed. As the species abundance in the higher bed was rather low, these data are not included in Fig. 11. The maxima in the curve in Fig. 11 were

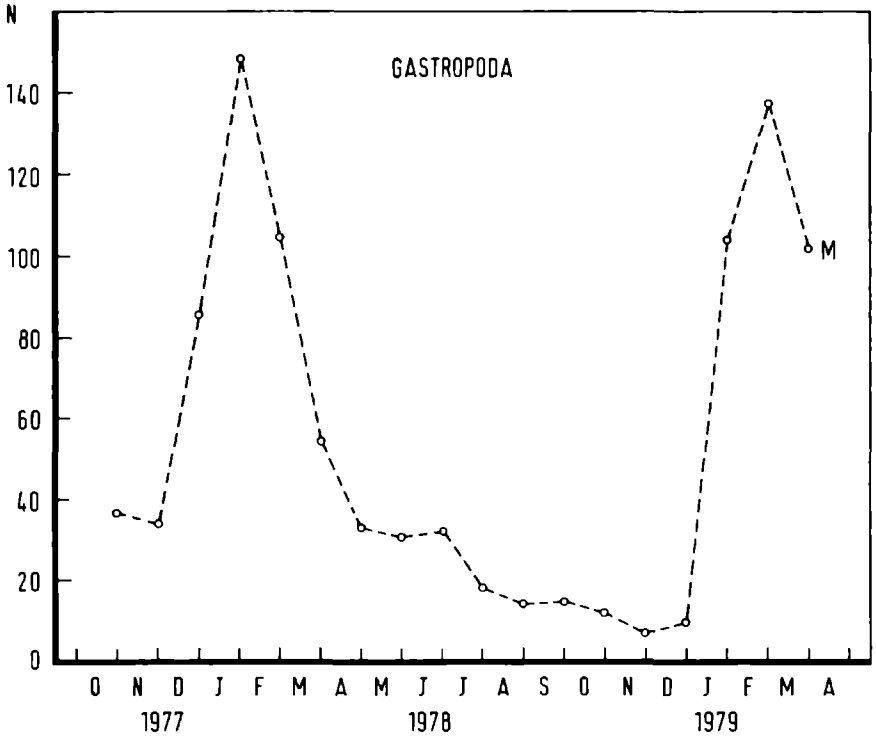


Fig. 11. See legend Figure 5.

caused by the most numerous species, Onoba semicostata and to some extent by Rissoa spp. O. semicostata only showed a pronounced decrease a few months after the spill, and therefore it does not seem justified to suggest any connection, as this may reflect an annual cycle. In fact, in February/March 1979 the species abundance and richness was of the same magnitude as the previous year.

Though Nelson-Smith (1968) reported that several species were most sensitive to oil pollution, the effects seem to be more a consequence of physical features interfering with settlement and loss of foothold than of toxic compounds (O'Sullivan and Richardson, 1967).

Bivalvia

Of the 14 incidentally recorded species (Tables 5 and 6), Loripes lacteus was most common in the higher bed, while Lucinoma borealis was found regularly in both beds though in lower numbers. In the middle bed the diversity was highest: more species occurring with a lower abundancy. In general the numbers of individuals decreased during the first three months after the spill, especially of Mysella bidentata and Abra spp. However, even the incidentally recorded bivalves did not disappear completely.

Periodic immersion in oil has been reported to have no noticeable effects on bivalves, though during large oil spills littoral species demonstrated an accumulation of petroleum hydrocarbons (Blumer et al., 1970; Straughan, 1977; Kineman et al., 1980).

Echinodermata

Amphipholis squamata appeared to be the dominant species in both beds, at least in the first months of the investigation period. Towards the end of 1978 the numbers decreased in the higher bed and from January onwards the species was never found, probably due to the newly deposited sand-layers (see p. 180). In the middle bed the numbers only decreased after April, reached very low values in June and July, and subsequently gradually increased (see Table 5). At the end of the observation period the winter maxima of 1977/1978 had not been reached.

Tunicata

Morchellium argus appeared to be the most common species, though Sidnyum turbinatum and Aplidium pallidum were found quite regularly. The other tunicates (see Table 6) were recorded only incidentally. After February 1978 tunicates no longer colonized the higher bed, probably for the same reason mentioned for the Echinodermata. All the species given in Table 6 were found both before and after the spill, though in fluctuating quantities.

DISCUSSION AND CONCLUSIONS

The data on the structural and functional aspects of the seagrass ecosystem, collected over a number of years and including a pre-spill and post-spill period, show the effects of the oil pollution to be selective. The effects on the seagrass itself were only observed locally during the first weeks following the spill, the normal processes related to growth, production and reproduction not being influenced. The species richness and abundance of the most important groups of benthic fauna appeared to have undergone a reduction. A significant decrease was seen in the Amphipoda and Echinodermata in particular. However, most species had attained their former level about one year after the spill; only the filter feeding amphipods did not reappear during the period of investigation. In Milford Haven (Wales) a refinery effluent was found to have no observable effects on a Zostera marina community (Baker, 1981).

Comparison of the results of this investigation with data on the impact of 'Amoco Cadiz' oil on other littoral communities is rather difficult. Depending on sediment type, exposition of a particular coastal area, methods employed in clean-up operations, etc., the influence of the spill differed considerably from place to place. All the authors mentioned in the Introduction of this paper reported a decrease in species abundance, whereas the species richness was not affected, the amphipods forming the only exception. Local effects on species abundance remained perceptible for at least the three years after the spill (Raffin et al., 1981). However, the fate-and-effects studies may have been disturbed severely by the offshore break-up of the 27,000 t tanker Tanio during spring 1980.

This study is only significant because baseline descriptions were also made. The impact of the 'Amoco Cadiz' oil spill on the seagrass ecosystem could only be assessed satisfactorily with reference to those data. Descriptive parameters such as diversity or productivity would seem irrelevant if no indication is given of species composition. For instance, a species may disappear and be replaced by an opportunistic species without causing any initial change in the diversity index. However, if the stability of the system is disturbed, the diversity index may show a resultant fluctuation with a gradually decreasing amplitude. The diversity index may thus help to determine the relative sensitivity of the ecosystem, and as a single statistic it may serve as an actual structural parameter. In this context the lower diversity values after the spill indicated an imbalanced community, but the numbers by themselves are meaningless. It is essential that the more common aspect of the functioning and dynamics of the system are understood, supported by an elucidation of habitat sensitivity rather than species sensitivity. In the case of the seagrass ecosystem the structure is most complex, with elements vertically arranged around the frame of the plant community (Jacobs and Huisman, 1982). The faunal diversity increases as the number of floristic elements increases. In general, the seagrass beds at Roscoff have a rather high diversity compared with other marine and brackish water communities (e.g. Marsh, 1973; Thayer et al., 1975; Lappalainen and Kangas, 1975; Verhoeven, 1980), as well as a high productivity and turn-over.

The general structure of the beds was not changed by the oil. Due to the situation in the tidal area, the contact between the oil slick and the eelgrass did not last longer than 6 h per day. Moreover, it seems likely that the plant community protected the benthic fauna from direct contact with the slick. The concentration of hydrocarbons in the seawater was 20 to 150 mg l^{-1} during the first three weeks (Marchand and Caprais, 1981), decreasing to 1-2 mg l^{-1} at the end of July (Laubier, 1980). The high concentration of dissolved compounds probably caused the observed mortalities. However, due to the firm and thick rhizome mat, mixing of oil and sediment was nearly impossible in the beds. This may account for the specific effect on the filter feeders which were permanently exposed to the oil in the seawater. The buffer effect of the seagrass becomes evident by comparing the results with those from areas without eelgrass beds, where bottom and oil were in direct contact (Chassé, 1978; Hyland, 1978).

The harm created by the spill caused only a short-term change in diversity, without really affecting the stability of the seagrass ecosystem. In contrast to long-term changes on other parts of the coast (see Chassé, 1979), the seagrass ecosystem appears more able to regain stability.

It may be concluded that the impact of the oil spill on the various groups of animals, except the amphipods, was only temporary. The high reproductivity of the survivors probably led to the rapid recovery of the populations, this in contrast to the situation after the 'Torrey Canyon' spill when recolonization had to occur by migration and settlement (Southward and Southward, 1978). However, had the Amoco Cadiz impact occurred in another season, the effects might have been substantially different. The reappearance of most amphipod species is much slower as these species must repopulate by migration from other areas. This process is slowed down by the hydrographical and topographical characteristics of the particular part of the coast. The dispersion of species with pelagic larvae is not hindered.

Several criteria have been proposed for ranking the sensitivity of areas to oil pollution (Owens, 1977, 1979; Gundlach and Hayes, 1978; Worbets, 1979). These criteria are mainly based on physical, geological or human factors, which are generally related to the vulnerability of the coastline with respect to the persistence of the oil. However, the ecological properties of an area do not always coincide with the physical susceptibility. A principal objective of sensitivity determination should be to recognize and classify susceptible areas according to ecological criteria (as also proposed by Cowell et al, 1979).

TABLE 6

Species list of animals found in the Zostera marina beds at Roscoff from October 1977 to April 1979 and their frequency of occurrence (in number of months, with a maximum of 19); p = species present.

Species	Higher Zostera bed (+ 3.4 m)	Middle Zostera bed (+ 2.8 m)
Porifera		
Halichondria bowerbanki Burton	p	p
Halichondria panicea (Pallas)	p	p
Haliclona limbata (Montagu)	p	
Hymeniacidon perlevis (Montagu)		p
Leucosolenia botryoides (Ellis & Solander)		p
Scypha raphana Schmidt		p
Anthozoa		
Anemonia sulcata (Pennant)	p	p
Cereus pedunculatus (Pennant)	p	p
Halcampa chrysanthellum (Peach)	p	p
Polychaeta Errantia		
Harmothoe impar Johnston		2
Harmothoe lunulata (Delle Chiaje)	3	8
Harmothoe spinifera Ehlers	2	2
Sthenelais boa (Johnston)	10	9
Eteone longa (Fabricius)	2	1
Eulalia sanguinea Oersted	1	
Phyllodoce mucosa Oersted	18	19
Amblyosyllis formosa Claparède		1
Autolytus prolifer (Müller)		2
Odontosyllis ctenostoma Claparède		2
Odontosyllis gibba Claparède		2
Syllis gracilis Grube	1	1
Syllis prolifera Krohn		1
Sphaerodorum gracile (Rathke)		4
Sphaerodorum peripatum Claparède		6
Micronereis variegata Claparède	1	1
Nereis caudata Delle Chiaje	1	2
Perinereis cultrifera (Grube)	5	
Platynereis dumerilii (Aud. & Milne-Edw.)	19	19
Nephtys hombergii Savigny	5	
Glycera alba (Müller)	5	1
Glycera convoluta Keferstein	1	
Lumbrineris latreilli Aud. & Milne-Edw.	18	17
Marphysa bellii (Aud. & Milne-Edw.)	1	1
Polychaeta Sedentaria		
Aonides oxycephala (Sars)	16	19
Malacoceros fuliginosus (Claparède)	9	8

Polydora antennata Claparède	1	
Polydora flava Claparède	17	10
Spio filicornis (Müller)	17	4
Caulleriella bioculatus (Keferstein)	6	1
Cirratulus cirratus (Müller)	6	
Cirriformia tentaculata (Montagu)	6	
Scoloplos armiger (Müller)	13	1
Capitella capitata (Fabricius)	4	
Heteromastus filiformis (Claparède)	11	16
Notomastus latericeus Sars	19	19
Arenicola grubii Claparède	1	
Arenicola marina (Linnaeus)	2	5
Euclymene oerstedi (Claparède) / Euclymene c.f. affinis (Sars)	19	19
Pectinaria koreni Malmgren		1
Amphicteis gunneri (Sars)		2
Amphitritides gracilis (Grube)	8	14
Eupolymnia nesidensis (Delle Chiaje)		6
Lanice conchilega (Pallas)	1	
Polycirrus aurantiacus Grube	1	1
Polycirrus medusa Grube		1
Thelepus setosus (Quatrefagus)		1
Chone collaris Langerhans		1
Megalomma linaresi (Rioja)	1	13
Megalomma vesiculosum (Montagu)	1	
Sabella penicillus Linnaeus		3
Sipunculida		
Golfingia elongata (Keferstein) / Golfingia vulgaris (de Blainville)	3	10
Pycnogonida		
Achelia echinata Hodge		3
Achelia hispida Hodge		1
Achelia longipes Hodge		1
Anoplodactylus angulatus (Dohrn)		5
Endeis laevis Grube		1
Nymphon gracile Leach		7
Decapoda		
Crangon crangon (Linnaeus)	1	
Hippolyte varians Leach		2
Processa edulis (Risso)		2
Achaeus cranchi Leach		1
Anapagurus brevicarpus (Bell)		1
Atelecyclus rotundatus (Olivi)		3
Carcinus maenas (Linnaeus)	13	15
Eurynome spinosa Hailstone		3
Macropipus arcuatus (Leach)		4
Macropodia rostrata (Linnaeus)		2
Pagurus bernhardus (Linnaeus)	1	1
Pagurus cuanensis (Thompson)		1

Pilumnus hirtellus (Linnaeus)		4
Pirimela denticulata (Montagu)		2
Pisidia longicornis (Linnaeus)		4
Amphipoda		
Ampelisca spinipes Boeck		3
Amphithoe rubricata (Montagu)		2
Amphithoe vaillanti Lucas		3
Ampelisca spinipes Boeck		3
Aora typica Kröyer		4
Apherusa bispinosa (Bate)		1
Apherusa jurinei (Milne-Edwards)		1
Caprella sp.		2
Coremapus versiculatus Norman		3
Dexamine spinosa (Montagu)		1
Dexamine thea Boeck		7
Elasmopus rapax A. Costa		2
Erichthonius brasiliensis (Dana)		1
Eurystheus maculatus (Johnston)		3
Gammarus locusta (Linnaeus)	2	2
Harpinia crenulata Boeck		4
Harpinia pectinata O. Sars		7
Jassa falcata (Montagu)	2	5
Lembos websteri Bate	1	6
Leucothoe incisa D. Robertson	5	2
Leucothoe spinicarpa (Abildgaard)		4
Lysianassidae spp.		5
Melita obtusata (Montagu)		4
Micropotopus longimanus Chevreux		2
Nototropus guttatus (A. Costa)		3
Pherusa fucicola Leach		14
Phthisica marina Slabber		2
Pleonexes gammaroides Bate		1
Podocerus variegatus Leach		2
Stenothoe monoculoides (Montagu)		7
Sunamphithoe pelagica (Milne-Edwards)		3
Urothoe grimaldii (Chevreux)	2	
Cumacea		
Bodotria scorpioides (Montagu)		2
Cumella pygmaea G.O. Sars		1
Iphinoe tenella G.O. Sars	5	10
Tanaidacea		
Apseudes latreillei (Milne-Edwards)	19	19
Apseudes talpa (Montagu)		10
Leptochelia dubia Kröyer		5
Isopoda		
Astacilla longicornis (Sowerby)		1
Dynamene bidentata (Adams)		3
Idotea chelipes (Pallas)		1

Idotea pelagica Leach		2
Janira maculosa Leach		5
Munna minuta Hansen		1
Paranthura costana Bate & Westwood		5
Gastropoda		
Acmaea virginea (Müller)		1
Alvania crassa (Kanmacher)		3
Barleeia unifasciata (Montagu)		2
Bittium reticulatum (Da Costa)	2	13
Calliostoma zizyphinum (Linnaeus)		3
Cerithiopsis tubercularis (Montagu)	1	6
Cantharidus striatus (Linnaeus)		1
Chauvetia minima (Donovan)		8
Cingula cingillus (Montagu)		2
Elysia viridis (Montagu)		2
Gibbula cineraria (Linnaeus)	1	5
Gibbula pennanti (Philippi)	7	14
Gibbula umbilicalis (Da Costa)	2	9
Helcion pellucidum (Linnaeus)		1
Hinia incrassata (Ström)	1	6
Hinia reticulata (Linnaeus)	2	6
Lacuna vincta (Montagu)		1
Lamellaria perspicua (Linnaeus)	1	3
Littorina obtusata (Linnaeus)	4	3
Littorina saxatilis (Olivi)	2	1
Mangelia attenuata (Montagu)		1
Mangelia costulata Risso		1
Ocinebrina aciculata (Lamarck)		10
Odostomia unidentata (Montagu)		3
Onoba semicostata (Montagu)	2	15
Retusa truncatula (Maton & Rockett)		3
Rissoa guerini Récluz	1	
Rissoa membranacea (Adams)		7
Rissoa parva (Da Costa)		7
Tricolia pullus (Linnaeus)		1
Bivalvia		
Abra alba (Wood)		3
Abra nitida (Müller)	1	5
Divaricella divaricata (Linnaeus)		1
Ensis ensis (Linnaeus)	1	
Laevicardium crassum (Gmelin)		1
Loripes lacteus (Linnaeus)	19	8
Lucinoma borealis (Linnaeus)	15	17
Mysella bidentata (Montagu)	4	17
Nucula nucleus (Linnaeus)		14
Parvicardium exiguum (Gmelin)	3	5
Thyasira flexuosa (Montagu)		1
Venerupis pullastra (Montagu)	1	
Venerupis senegalensis (Gmelin)	1	
Venus verrucosa Linnaeus		1

Echinodermata		
Amphipholis squamata (Delle Chiaje)	4	19
Asterina gibbosa (Pennant)		1
Ophiura albida Forbes		1
Tunicata		
Aplidium pallidum (Verrill)		p
Botryllus schlosseri (Pallas)		p
Didemnidae		p
Morchellium argus (Milne-Edwards)	p	p
Sidnyum turbinatum Savigny		p

ACKNOWLEDGEMENTS

I would like to thank John Stassen, Wim Buys, Willibrord Huisman, Liesbeth Pierson, Yvonne Jeuken, Wim Quax, Niek Manders and Toine de Jong for providing practical assistance throughout this study. I am also indebted to Prof. Dr. C. den Hartog and Ir. J. van der Harst for critically reviewing the manuscript, Dr. Connie A.N. van Oorschot for correcting the English text, Theo Oor and Marcel Kuppens for preparing the drawings and Dora Williams, Ans Wijsman and Ingrid Rietdijk for typing the manuscript. Mr. J.C.M. Dieleman, Mr. J.C. den Hartog, Dr. R.W.M. van Soest, Dr. G. Hartmann-Schröder and Mr. A.W.M. Lacourt helped with the identifications of the amphipods, sea-anemones, sponges, polychaetes and bivalves, respectively. A great part of the practical work was carried out at the Station Biologique at Roscoff; I thank the director, Prof. Dr. J. Bergerard and the staff for their hospitality. The first part of the investigation (to April 1978) was made possible by financial support from the Netherlands Organization for the Advancement of Pure Research (ZWO), the second part was financed by the Shell Internationale Research Maatschappij B.V.

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COMPILATIE VAN STUDIES OVER ZEEGRAS-OECOSYSTEMEN
LANGS WEST-EUROPESE KUSTEN

SAMENVATTING

Zeegrassen zijn monocotyle angiospermen die in mariene en brakke wateren over de gehele wereld voorkomen. Deze groep waterplanten omvat momenteel ca. 50 soorten binnen twee families. Langs de kusten van West-Europa zijn slechts twee vertegenwoordigers te vinden: Zostera marina L. en Zostera noltii Hornem. Beide soorten zijn wijd verbreid: van de Noorse Atlantische kust en het Kattegat in het noorden tot de kusten van Spanje en Portugal in het zuiden. In de Oostzee dringt Z. marina binnen tot ongeveer de zestigste breedtegraad. Beide soorten vormen submerse vegetaties in brakke binnenwateren, maar komen het meest voor in ondiepe kustwateren. Z. noltii wordt daar alleen aangetroffen in het getijgebied, terwijl Z. marina zowel in het getijgebied als in het sublittoraal voorkomt. Naast het genoemde verschil in standplaats, wordt de variabiliteit binnen het zeegras-oecosysteem nog eens benadrukt door het ruimtelijk gescheiden voorkomen van éénjarige en overjarige populaties van Zostera marina.

In dit proefschrift zijn de resultaten weergegeven van een oecologische studie van strukturele en funktionele aspekten van zeegras-systemen, die karakteristiek zijn voor de verschillende habitat-typen. De belangrijkste onderzoeksterreinen waren de wadden ten zuiden van Terschelling (Waddenzee) en de slikken in de Krabbenkreek (Oosterschelde) in Nederland, en de kust bij Roscoff (Bretagne) in Frankrijk.

Struktureel gezien bleek de complexiteit van de zeegras-gemeenschap bijzonder groot te kunnen zijn. Rond de struktuurelementen van de dominante plant, het zeegras zelf, bleken vertikaal gerangschikte compartimenten te onderscheiden. De aanwezigheid van de verschillende onderdelen én de diversiteit binnen elk compartiment bleken gecorreleerd met de mate van waterbedekking. Een dergelijke relatie is in de eerste plaats geconstateerd voor het zeegras, waarbij de lengte

van de planten en het aantal planten per oppervlakte-eenheid als parameters onderscheiden konden worden. Het bleek dat bij een toenemende waterbedekking de biomassa per m^2 toenam en het aantal planten per m^2 afnam, terwijl de lengte ervan toenam. De ontwikkeling van de bloeiwijzen vertoonde een positieve correlatie met toenemende waterbedekking. Dit verschijnsel én de ontwikkeling en rijping van bloemen en vruchten zijn gedetailleerd beschreven in relatie tot de ontwikkeling van de gehele bloeistengel.

Bij toenemende diepte werd de samenstelling van de floristische elementen binnen de gemeenschap complexer en bleek gecorreleerd met geringere fluktuaties van abiotische faktoren. Als meest belangrijke struktuur-elementen werden onderscheiden: het zeegras zelf met de bladeren, de bundel bladscheden en de rhizoommat, de epifytische algen op de zeegrasbladeren en de algenmat tussen de zeegrasplanten. De mate van voorkomen van deze elementen was van grote invloed op de diversiteit van de macrofauna. Zo bleek de fauna hoog in het getijgebied, bij een gering aantal floristische elementen, gekarakteriseerd door een lage diversiteit en een soortensamenstelling die nauwelijks afweek van de omringende, niet door zeegras begroeide substraten. In dergelijke velden behoorde het overgrote deel van de dieren tot eenzelfde trofisch niveau, de 'deposit feeders'. In lager gelegen velden ging een toenemende diversiteit van de floristische elementen samen met een grotere rijkdom van de fauna, terwijl de dieren meer gelijkmatig over de verschillende trofische niveau's verdeeld waren.

Ter bestudering van de produktiviteit van het zeegras is gebruik gemaakt van de eigenschappen betreffende vegetatieve morfologie en groei van de planten, waarbij het Plastochron Interval (P.I.: het tijdsinterval tussen het verschijnen van twee opvolgende bladeren aan een plant) de maat voor de produktiesnelheid vormde. Op deze wijze kon een nauwkeurig overzicht worden verkregen van de produktie van de afzonderlijke plantedelen en van de totale produktie in de overjarige Bretonse zeegrasvelden. Doordat deze gegevens gedurende verschillende seizoenen werden verzameld, kon geconstateerd worden dat de produktie

van fotosynthetiserend weefsel direkt gecorreleerd was met de hoeveelheid instraling. Hoewel er in de Nederlandse zeegrasvelden wel gegevens betreffende biomassa, bedekking en bloei zijn verzameld, bleken produktiemetingen, zoals uitgevoerd bij Roscoff, onmogelijk. Dit was niet alleen het gevolg van het éénjarige karakter van de Zostera marina vegetaties in de Waddenzee en de Oosterschelde, maar ook van de sterke begrazing van beide zeegrassoorten door watervogels gedurende de herfst en winter. Deze consumptie kon berekend worden op ongeveer 50% van de maximale 'standing crop'. Het niet direkt geconsumeerde organische materiaal verdween via de decomposer voedselketen.

Inherent aan de hoge 'turnover' bij een vrij constante biomassa was een relatief korte levensduur van de zeegrasbladeren (gemiddeld 97 dagen), hetgeen belangrijke consequenties had voor de epifytische algen. Daarom konden, naast de strukturele opbouw, ook verschijnselen als kolonisatie en successie binnen de epiphytische gemeenschap bestudeerd worden.

Gedurende de onderzoeksperiode vond voor de kust van Bretagne de ramp met de olietanker 'Amoco Cadiz' plaats, waardoor de zeegrasvelden enige weken vooral gedurende de laagwater perioden in direkt contact kwamen met de ruwe olie. In het laatste hoofdstuk is een gedetailleerd overzicht gegeven van de effekten op het oecosysteem, waarbij vergeleken kon worden met de situatie voor deze ramp. Direkte effekten van de olievervuiling op het zeegras zelf bleken van zeer tijdelijke aard te zijn. De gevolgen voor de bentische fauna daarentegen waren ernstiger. Toch trad er binnen een jaar herstel op, waarbij de Amphipoda een uitzondering vormden. Op grond van vergelijking met de effekten op andere gemeenschappen in het getijgebied kon geconcludeerd worden dat het zeegras een beschermende habitat vormde, waarbij de planten als een buffer fungeerden tussen waterlaag en bodem.

CURRICULUM VITAE

René Petrus Wilhelmus Maria Jacobs werd op 28 maart 1948 geboren te Nijmegen. Zijn vroege jeugd heeft hij in Cuyk doorgebracht. Middelbaar onderwijs volgde hij aan het Canisius College te Nijmegen, waar hij, na een gymnasiale basis van vier jaren, in 1968 het diploma H.B.S.-B behaalde. In september 1968 liet hij zich inschrijven als biologiestudent aan de Katholieke Universiteit te Nijmegen.
Van september 1969 tot september 1970 moest de studie onderbroken worden voor het vervullen van de militaire dienstplicht, hetgeen resulteerde in een volleerde landmeter. Het kandidaatsexamen werd afgelegd op 6 juni 1972.

In het kader van de doktoraalstudie werd in 1973 een hoofdvak Dieroecologie bewerkt onder supervisie van Dr. H.C.J. Oomen en onder direkte leiding van Dr. A.M.J. Bouwhuis. Dit omvatte een onderzoek naar de populatie-dynamiek van de calanoide copepode Eudiaptomus vulgaris. Deze samenwerking moest helaas door het overlijden van Tonny Bouwhuis vroegtijdig worden afgebroken.

In 1974 bestudeerde hij onder leiding van Dr. C.K. Stumm en onder supervisie van Prof. Dr. Ir. G.D. Vogels de chemotaxis van gameten en zygoten van Allomyces arbuscula (bijvak Microbiologie). Onder supervisie van Prof. Dr. H.F. Linskens en Dr. Ir. G. van den Ende werd op het Unilever Research Laboratorium te Duiven onder direkte leiding van Drs. W.J. Kooiman de hitteresistentie van Bacillus subtilis onderzocht (bijvak Botanie).

Het doktoraalexamen werd cum laude afgelegd op 4 november 1975 en op 17 november van dat jaar werd hij aangesteld als wetenschappelijk medewerker ZWO aan het Laboratorium voor Aquatische Oecologie van de Katholieke Universiteit te Nijmegen. Deze aanstelling duurde tot 15 november 1979. Onder leiding van Prof. Dr. C. den Hartog werd een promotie-onderzoek verricht naar de oecologie van zeegrasgemeenschappen langs de kusten van Nederland en Frankrijk. Een deel van de resultaten daarvan is in dit proefschrift neergelegd. Gedurende de contractperiode assisteerde hij in Roscoff (Frankrijk) de jaarlijkse cursus "Mariene Biologie" voor de post-kandidaten van de Afd. Aquatisch Oecologie.
In maart 1978 werd hij geconfronteerd met de olieramp van de "Amoco Cadiz" voor de kust van Bretagne, waardoor het accent van het onderzoek aldaar verlegd moest worden naar de bestudering van de gevolgen van de olieverontreiniging, waarvoor de Shell Internationale Research Maatschappij B.V. een subsidie ter beschikking stelde.

In september 1978 werd een voordracht gehouden te Jerusalem (Israël) in het kader van het "Second International Congress of Ecology" met als titel: "Distribution and aspects of the production of eelgrass, Zostera marina L., at Roscoff (France)".
In oktober 1979 werd deelgenomen aan de jaarvergadering van de "International Council for the Exploration of the Sea" (Warsaw, Poland) met de bijdrage: "Effects of the Amoco Cadiz oil spill on the seagrass community at Roscoff (France) with special reference to the benthic infauna".
In november 1979 werd het Internationaal Symposium over de Amoco Cadiz te Brest (Frankrijk) bezocht.

Van 15 april 1980 tot 1 mei 1982 was hij als wetenschappelijk ambtenaar aangesteld aan het Centraalbureau voor Schimmelcultures te

Baarn (een instituut van de Koninklijke Nederlandse Akademie van Wetenschappen) belast met het onderzoek naar de taxonomie van waterschimmels en met name van de Oomyceten.

In januari 1981 werd een voordracht gehouden te Brussel (België) in het kader van het "International Colloquium on Aquatic Vascular Plants" getiteld: "Reproductive strategies of two seagrass species (Zostera marina en Z. noltii) along West European coasts".
In april 1981 volgde een bezoek aan het "International Colloquium on Aquatic Mycology" te Portsmouth (Engeland).

Sinds 1 mei 1982 is hij als wetenschappelijk adviseur milieu-toxicologie in dienst van de Afdeling Toxicologie van de Shell Internationale Research Maatschappij B.V. te 's Gravenhage.

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STELLINGEN

I

Aan het gebruik van de verleden tijd in het boek Genesis en met name in de frasen in het scheppingsverhaal 'En God zag dat het goed was', moet enige profetische waarde gehecht worden

II

De presentie van een generatieve fase in de levenscyclus van het zeegras *Zostera marina* is een direkt gevolg van ongunstige abiotische milieuomstandigheden en is eerder gericht op overleving dan op overdracht van genetisch materiaal of de verspreiding van de soort

Dit proefschrift

III

Het vermogen van zeegras tot het invangen van gesuspendeerd materiaal en de daarmee samenhangende effekten op de bodemgesteldheid houden tevens een zekere vorm van zelf-vernietiging in.

IV

Het verschijnsel 'heterothallie' in verband met de generatieve reproduktie van Oomyceten (waterschimmels) berust slechts op een onvermogen van de schimmels tot adequate produktie van specifieke induktoren

V

De methode om naar fysische en geomorfologische maatstaven de kwetsbaarheid van kustgebieden voor verontreiniging vast te stellen, is de laatste jaren steeds meer in zwang gekomen, doch houdt als zodanig te weinig rekening met biologische waarden en is daarom verwerpelijk

E R Gundlach en M O Haves, 1978 Mar Tech Soc J , 12(1)· 18-27

VI

Het is mogelijk toekomstige oecologen wetenschappelijk onjuiste conclusies te besparen en meer arbeidsvreugde te bezorgen wanneer taxonomen meer de moeite zouden nemen bij hun systematisch onderzoek ook oecologische aspekten te betrekken

VII

Het aanwijzen van indikator-organismen ter bepaling van de mate van biologische verstoring dient te gebeuren op grond van hun belang voor het funktioneren van het oecosysteem en niet naar esthetische of zeldzaamheids-maatstaven

VIII

Op grond van de invloed van licht en windrichting op de verdeling van plankton in stilstaande, ondiepe wateren, dient een visser bij voorkeur 's ochtends met de neus in de wind te hengelen.

IX

Uitgaande van een oecosysteem-benadering als basis voor economische ontwikkeling, dient de VVD als de meest natuurlijke binnen het Nederlandse partijenstelsel beschouwd te worden.

F. Vester, 1982. Milieu en Recht, 6: 146-154.

X

Het gebruik van hoog-gekwalificeerde terminologie om vaag-gekwalificeerd personeel aan te trekken kan omschreven worden als een kwalijke vorm van advertentie-vervuiling.

R. P. W. M Jacobs